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NOTE ON THE FOOD OF FISH IN HAWESWATER (WESTMORLAND)

BY G. H. SWYNNERTON AND E. B. WORTHINGTON
Freshwater Biological Association, Wray Castle, Ambleside

1. INTRODUCTION

THE food of trout and of a few other freshwater fish has been studied intensively by several workers in recent years, but for Britain there exist few data on which to base a comparison between the diet of two or more species of fish inhabiting the same water. The two papers by Allen (1935, 1938) on perch and trout in Windermere appear to be the fullest on this subject. This note, although based on an isolated set of observations, provides some information concerning four species of fish in the same water, namely, Lord Lonsdale's char (*Salvelinus alpinus lonsdalii* Regan), skelly (*Coregonus clupeoides stigmaticus* Regan), brown trout (*Salmo trutta* L.) and perch (*Perca fluviatilis* L.).

The fish were taken on 6 July 1938, in a seine fished from the south shore of Haweswater in the neighbourhood of the delta built up by Measand beck. The net had a mesh of $\frac{1}{4}$ in. (knot to knot) so that the method was not selective in regard to the size of fish. 24 char, 10 skelly, 102 trout and 79 perch were taken, and all were subjected to stomach examination except 1 trout and 21 perch. All the fish (see Table 1) were rather small, but this is in accord with the experience of those who angle on this lake (see Watson, 1925). In addition to these four species, a large number of minnows (*Phoxinus phoxinus* (L.)) and sticklebacks (*Gasterosteus aculeatus* L.) and several eels (*Anguilla anguilla* (L.)) were taken in the netting operations. The lake is stated to contain no pike (*Esox lucius* L.), and it appears doubtful whether salmon (*Salmo salar* L.) enter it from the River Eden via the River Lowther.

This examination of the fish in Haweswater was part of a programme of work carried out on the lake in 1938 prior to the impounding of its water as a great reservoir for the supply of Manchester. The object was to record the conditions as they were immediately prior to the raising of the water level, and then to carry out re-examinations at intervals in order to follow through the changes in biological conditions in subsequent years, when a large area of grassland in the Mardale valley will be flooded. Changes are expected in the food supply and growth rate of the fish, so the growth rate of the 102 trout taken has been determined from the examination of scales. The result of that study is to be published elsewhere together with similar data for other waters in the Lake District. The examination of the stomach contents was carried out by Swynnerton while working as a visitor at Wray Castle in 1938. The data have been analysed and presented by Worthington.

2. Methods

Various methods can be adopted in recording the contents of fish stomachs. Individual species comprising the food may be counted, or they may be weighed wet or dry, or their volume may be measured. The several processes take much time, and it is doubtful how far results justify the labour except in special detailed work. No detailed estimations of the quantity of each kind of food were attempted in the present study, because it was thought that the following rough method gave sufficient accuracy for our purpose. The contents of each stomach (not the intestine) were washed out, the various organisms were determined to species or to groups where detailed identification was impossible, and then on the basis of rough counts and judgment by eye each kind of food was designated as "very common", "common", "frequent", "rare" or "very rare". In this arbitrary classification due regard was taken to the size of individual food organisms; thus a stomach containing say 10 *Valvata piscinalis* and 30 *Bosmina longirostris* would be designated as "*Valvata* common, *Bosmina* frequent".

The contents of all stomachs, arranged in size groups for each species of fish, were then tabulated, and as a further approximation the two categories "very common" and "common" were designated together by a figure 3, "frequent" by 2, "rare" and "very rare" by 1. The integers in each section of the table were then added together and scaled down to the percentage basis, for presentation in the table. Since feeding conditions for freshwater fish vary so greatly from one environment to another, it is suggested that, in our present state of knowledge, large numbers of stomach examinations from many different waters, examined quickly in the way described, would be more valuable as a contribution to knowledge of fish and fisheries, than small numbers examined in great detail.

3. Results

The food materials in the left-hand column of the table are arranged roughly in order of size (with the exception of the last three items), so it may be seen at a glance that, for fish of roughly the same size, char and skelly feed on very small organisms, trout on those of intermediate size, while perch, except in the young stages, feed on larger food.

Taking the columns in the table in order, left to right, the 24 *char* have not been divided into size groups, as have the trout and perch, because no significant differences were found between the food of the smallest specimens, 12 cm. long, and the largest, 19·5 cm. They were feeding predominantly on Cladocera (65% of food). Of these organisms found in the stomachs the bulk was made up of one of the smallest waterfleas, *Bosmina*, and the rest were the large predaceous forms, in order of frequency *Polyphemus*, *Leptodora* and *Bythotrephes*. The Copepoda were represented only by *Cyclops*. Small aquatic insects, Chironomidae and Ephemeroptera nymphs, constituted about one-

quarter of the stomach contents; but other kinds of food occurred very sparingly. Regarding the food of this species Regan (1911) states "this char is said to feed mainly on insects and to take the artificial fly freely". The results above suggest, however, that *Salvelinus alpinus lonsdalii* in Haweswater, like *S. alpinus willughbii* (Günther) in Windermere is predominantly a plankton eater.

Table 1. *The food of fish in Haweswater*

		Skelly	Trout				Perch			
Length to fork of tail (cm.)	Char 12–20	20–24 (+one 37)	10–15	15–20	20–25	25–30	12–15	15–20	20–25	25–30
No. of stomachs examined	24	10	10	58	30	4	11	30	13	4
No. of stomachs empty	—	—	—	—	1	—	1	—	1	3
Copepoda	1	19	—	—	—	—	19	—	—	—
Cladocera	65	41	2	2	0·5	—	16	11	2	—
Hydracarina	2	10	—	2	2	—	—	—	—	—
Gammarus	—	—	—	1·5	—	—	4	9	2	—
Diptera, Chironomidae (larvae, pupae and a few adults)	10	6	20	19	18	7	23	23	17	—
Ephemeroptera (nymphs)	17	3	34	30	32	7	28	43	37	—
Plecoptera (nymphs)	—	—	—	—	0·5	—	—	2	—	—
Trichoptera (larvae and pupae)	—	1	12	9	4	7	4	8	—	—
Odonata, Agrionidae nymphs	2	—	—	—	—	—	—	—	—	—
Corixidae (*Micronecta*)	—	—	8	0·5	—	—	—	—	—	—
Coleoptera (? water beetles)	—	—	18	11	18	27	—	—	—	—
Surface insects	2	—	2	2	0·5	—	—	—	—	—
Mollusca	—	18	4	16	11·5	20	—	—	—	—
Fish	0·5*	1*	—	0·5*	4	20	6	—	36	100
Algae	—	1	—	2	1	—	—	1	4	—
Vegetable (other than algae)	—	—	—	4	6	12	—	2	—	—
Incidental (stones, bark, etc.)	0·5	—	—	0·5	2	—	—	1	2	—

* Scales only, perhaps swallowed accidentally after capture.

The figures represent percentages of each kind of food for each species and size group of fish (vertical columns add to 100)

The *skelly*, represented by nine smallish specimens of length between 20 and 24 cm. and one large specimen of 37 cm., have been grouped together in the table. Like the char they had fed mainly on small Crustacea, but there was the striking difference that the skelly had eaten a large quantity of Copepods, mainly *Cyclops* but mixed with some *Diaptomus*. Of the Cladocera only *Leptodora* among the large predators had been eaten by skelly, but *Eurycercus*, *Alona* and *Sida*, none of which had occurred in char, were prominent. These facts suggest that the skelly and char, although inhabiting the same area of water and having a general similarity in their food, do not compete directly with each other. From the fact that Mollusca (*Valvata piscinalis* (Müll.)) provided 18% of the skellies' food and none of the chars', and that Hydracarina, which are typically weed-dwellers, provided 10% of the skellies' food and only 2% of the chars', it may be assumed that skelly were feeding nearer the bottom, probably in and around the beds of weed. This conclusion is borne out by the different kinds of Cladocera in the stomachs. Of those in the char *Bythotrephes*, *Leptodora* and probably *Bosmina* are typically planktonic forms; only *Polyphemus* is an inhabitant of the weed beds. Of

those in the skelly *Eurycercus*, *Alona* and *Sida* are typical weed-dwellers, although the presence of *Leptodora* and the Copepod *Diaptomus* indicates that some of the skellies had made excursions into the planktonic zone. The conclusion is reached that, in the case of these two species of fish, the differences in food can be explained by the selection of different feeding grounds, and there is no reason to assume that the fish select individual organisms.

The above observations confirm the statements of Regan (1911) and other authors that the skelly, like its close relative the powan (*Coregonus clupeoides* Lacepède) of Loch Lomond, feeds mainly on Entomostraca. It cannot be assumed, however, that it habitually feeds on or near the bottom, because both species have often been observed in shoals on the extreme surface, especially late in the evening. It may be suggested that these Coregonids feed at times on the true plankton, and, following the diurnal vertical migrations of the plankton, come close to the surface at night. The skelly is known only from Haweswater, Ullswater and Red Tarn on Helvellyn. The nature of its food prevents its frequent capture by anglers and therefore it has acquired the unjustified reputation of being very rare.

The 101 *trout* have been divided into four size groups in order to show how far the food changes with increasing size. The table shows that within the range of size available there was little change in the character of the diet, except in regard to the largest size group, 25–30 cm., of which there were only four individuals. This is in conformity with the results of other workers, notably of Allen (1938). It is a little surprising that Cladocera were so inconspicuous in the stomachs, the only kinds found being *Eurycercus* and *Bosmina*. The bulk of food of all trout except the largest size group consisted of the temporary bottom fauna, especially insects: Ephemeroptera nymphs (especially Baetidae and Caenidae) were the most important, and Chironomidae next. The figures for Coleoptera (water-beetles) must be accepted with reserve because the remains of beetles in fish stomachs are difficult to identify and in some cases casual land beetles taken on the surface may have been entered as water-beetles in error. The "surface insects" were all casual Diptera, Hymenoptera and Coleoptera, and in view of the time of year it is rather surprising that this kind of food constituted so small a proportion of the whole. Mollusca provided a considerable part of the food of the larger trout: they consisted mainly of *Valvata piscinalis* (Müll.), but a few *Limnaea peregra* (Müll.), *Ancylastrum fluviatile* (Müll.) and a small species of *Planorbis* were also found. Fish food (stickleback and probably minnow) were important only in the largest size group. An appreciable amount of vegetable material had been eaten by some of the larger trout, but little significance can be attached to the records of algae, which were found free in a few stomachs, because these may have been liberated by digestive processes from the interior of invertebrates.

The *perch* showed a pronounced change in diet as their size increased: the

smaller specimens were feeding to a large extent on planktonic Crustacea, those of intermediate size on aquatic stages of insects and the larger specimens on fish. This conclusion is the same as that of Allen (1935) in his detailed work on the food of perch in Windermere, except that the size at which the changes in feeding habit takes place in Haweswater appears to be rather larger than in Windermere. This is perhaps related to the fact that perch in Haweswater are generally of a larger size than those of Windermere. As in the case of trout, Ephemeroptera nymphs and Chironomidae were the staple food of perch, but apart from these it is noteworthy that the two species seem to have been competing very little: small Crustacea and *Gammarus* were eaten extensively by perch but very little by trout, whereas Mollusca and water-beetles provided much food for trout but none for perch. These differences in food suggest that either the perch and trout were selecting different feeding grounds, or that they were selecting different organisms on the same feeding ground. If the former is correct, it must be assumed that places where perch were feeding contained *Gammarus*, but few Mollusca and water-beetles, while places favoured by trout had plenty of Mollusca and water-beetles, but few *Gammarus*. From what is known of the distribution of invertebrate fauna it seems unlikely that such faunistic differences exist on a limited area of lake floor, so it is probable that selection of individual food organisms accounts for the difference in diet between perch and trout.

We are indebted to the Hon. Anthony Lowther for facilities in netting the fish from Haweswater, and to members of the Freshwater Biological Association's staff for helpful criticism.

4. Summary

The examination of 194 stomachs of fish netted on one day from Haweswater gives some indication of the degree of competition for food between four species of fish. Char (*Salvelinus alpinus lonsdalii*) and skelly (*Coregonus clupeoides stigmaticus*) had both fed predominantly on Entomostraca, but for the most part had taken different species, so that there was little overlap in diet. There were indications that the char had fed mainly on the plankton, while the skelly had been feeding nearer the bottom, around beds of weeds.

Brown trout (*Salmo trutta*) and perch (*Perca fluviatilis*) had eaten larger food and here again there was some indication that the two kinds of fish had either selected different feeding grounds or different organisms on the same feeding ground. The latter explanation is the more likely.

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THE FAUNA OF THE RIVER MELINDWR, A LEAD-POLLUTED TRIBUTARY OF THE RIVER RHEIDOL IN NORTH CARDIGANSHIRE, WALES

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(*With* 1 *Figure in the Text*)

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1. Introduction

From prehistoric times until the beginning of the twentieth century, lead-mining and the crushing and washing of the ore (galena) was one of the chief industries of north Cardiganshire. During the first half of the nineteenth century the industry flourished, but after 1872 it declined under the influence of foreign competition and in 1900 nearly all the mines had been closed down. A small number were reopened during the period of the Great War, but this revival was temporary and at the present time lead-mining in Cardiganshire is a dead industry.

The extraction of the ore was accomplished by crushing or grinding the mined material into a fine state of division and washing the crushed material with running water which carried off the lighter earthy impurities leaving behind the heavy galena. As might be expected, the separation of galena and earthy particles was not complete, so that the washing water carried off quantities of galena in a fine state of division. Apparently it was the ancient practice to allow the washing water to flow directly into the neighbouring rivers and streams, which carried the finely divided ore for considerable distances before it was finally deposited on their beds, or, at flood time, on land bordering their banks. Later, when the poisoning of domestic animals, especially horses, poultry and ducks, and the wholesale destruction of pasture land which resulted from this practice had aroused serious concern, the

precaution was taken of leading the washing water through series of settling ponds in which most of the suspended material was deposited before the water reached the streams. The material collecting in the settling ponds, and mined material too poor in galena for its extraction to be profitable, remains piled up as the grey lead-mine dumps which are a characteristic feature of the valleys of north Cardiganshire.

One of the largest and richest of the Cardiganshire mines was the Goginan Mine, situated about six miles east of Aberystwyth and on the banks of the river Melindwr, a tributary of the river Rheidol. This mine was closed in 1886, reopened in 1919 and finally abandoned in 1922. The mine dump is of considerable size, contains material in all stages of division ranging from large rough blocks to fine slimes, and for a short distance actually forms the north bank of the stream. Much of the dump material contains about 1·5% of lead sulphide, and during dry weather this appears to become oxidized slowly to form soluble lead sulphate which subsequently is dissolved by rain water running over or seeping through the dump and so reaches the river. Thus, seventeen years after the cessation of mining activity, the Melindwr continues to be polluted with lead in solution and also by solid dump material washed into the stream by the water draining the dump, by finely divided solid material carried by north and east winds, and as a result of the weathering of the bank.

In 1922, 1924, 1925 and 1926 Carpenter published a series of papers showing how the fauna of a number of Cardiganshire streams was affected by effluents from the lead mines; and the writer, in collaboration with Prof. R. Douglas Laurie (Laurie & Jones, 1938), has described the faunistic recovery of the Rheidol. In 1919 this river was heavily polluted and almost barren of fauna and flora. As a result of the cessation of mining activity and gradual consolidation of the mine dumps upon its banks, with consequent diminution in the degree of pollution, the river has materially recovered, so that at the present time it carries a rich and varied fauna, including fish. No records appear to exist regarding the fauna of the Melindwr and the present paper describes the results of an investigation undertaken in 1939 to ascertain how far, and how selectively, the fauna of the Melindwr appears to be limited by the dissolved lead salts and the solid materials that enter the river at the Goginan Mine.

2. Topography

A complete map of the Rheidol and its tributaries is to be found in Laurie & Jones (1938).[1] The source of the Melindwr is a reservoir, Pond Syfydrin, situated at an altitude of about 1000 ft. on the western edge of the Plynlimon Plateau. A little over a mile from its source the stream is joined by a tributary from another reservoir, Llyn Castell Coch, and then cascades southwards into

[1] For reasons connected with the war, the detailed maps of the river Melindwr are not published here. They are deposited for reference in the University College of Wales, Aberystwyth. Editor.

a narrow, gorge-like, glaciated valley. Later it turns westwards and flows more gently through a wider valley of fertile cultivated land to join the Rheidol at the village of Capel Bangor, four and a half miles from Aberystwyth where the Rheidol reaches the sea. Throughout its course the Melindwr is rapid in flow and its bed is stony or rocky, composed mainly of weathered pebbles and large stones. No natural backwaters exist and except at certain points where artificial barriers have been erected to divert the water into channels to run water wheels there are no pools of any size.

The rocks of the neighbourhood contain very little limestone and the water of the stream has a very low calcium content. As it arises from reservoirs, the stream maintains a good flow even during long periods of dry weather, though its tributaries rapidly dry up at such times. The water is slightly acid (*p*H 6·6–6·8) and except when rendered turbid at time of flood, is clear and contains little suspended matter. The climate is equable; generally colder on the plateau, where the rainfall greatly exceeds that of the coastal area and where heavy snowfalls are frequent in winter.

3. Sources of pollution

The main source of pollution by dissolved and solid material is the dump of the Goginan Mine. This lies to the north of the river, sloping gently in its direction, and for about 90 yards actually forms its right bank. The dump is drained by a series of water channels (*C*), which probably carried the effluents from the settling pits when the mine was in active operation; but no water now flows along these channels except at times of very abnormal rainfall. A few yards below the point where this system of water channels enters the river the latter is joined by a small streamlet which issues from a culvert (*CL*).

Where it skirts the mine dump, and for a distance of some 50–60 yards beyond, the stony stream bed is thickly carpeted with the grey mine dump material, which also fringes both its margins. No phanerogams appear to be able to grow on such a substratum and this part of the stream appears to be completely devoid of vegetation. Further down the silt gradually disappears, the stream bed is once more composed of clean stones and pebbles, and is fringed by the grasses of the neighbouring pastures.

About half a mile above the Goginan Mine the Melindwr receives a small tributary, the Nant Brwyno, which drains from the disused Cwm Brwyno lead mine. This stream arises as a seepage from the Cwm Brwyno mine dump and is heavily polluted with dissolved lead, but is normally small in volume and during dry weather dries up completely. Solid dump material is carried by the Nant Brwyno for a short distance only, and none appears to reach the Melindwr. The other mines in the Melindwr basin are small, contain no dumps of finely divided material, and do not constitute appreciable sources of pollution so that above its confluence with the Nant Brwyno the Melindwr is unpolluted.

A number of analyses of the water of the river and its tributaries have been made and the results are given in Table 1. The analyses were made by the adsorption-colorimetric method of James (1929). The results show that the river is most heavily polluted immediately below the Goginan dump, the dissolved lead content varying from about 0·05 mg. per litre during dry weather to 0·3 mg. per litre after rain. Nearer the Rheidol the degree of pollution is lessened by dilution by unpolluted tributaries and above the confluence the lead content varies from a trace to 0·1 mg. per litre.

Table 1. *Analyses of the water of the Melindwr and its tributaries*

Date 1939	Locality	mg. Pb per litre	Remarks
27 June	Below the dump at Goginan (*E*)	0·05	Water level low after a period of dry weather
14 „	„	0·3	Slight flood after one day of heavy rain
17 „	„	0·12	Flood subsiding
4 July	„	0·05	Water level normal on day of slight and intermittent rain
8 „	„	0·2	After two days' heavy rain and with the river in full flood
6 June	Near the confluence with the Rheidol (*A*)	0·02	River level normal
8 July	„	0·1	After two days' heavy rain and with the river in full flood
2 „	Nant yr Arian (*K*)	Trace?	Slight flood on day of intermittent rain
2 „	Nant Brwyno (*L*)	0·5	Slight flood on day of intermittent rain
4 „	„	0·6	Stream level normal
5 „	„	0·6	Stream level normal
2 „	Melindwr above the lead mines (*G*)	Nil	Slight flood

4. Survey of the fauna

(*a*) *Collecting stations*

The fauna of the stream was studied at seven selected stations, the general characters of which are as follows:

A. Immediately above the confluence with the Rheidol. Here the bed of the stream is very irregular, the water rushing over large stones at some points and at others flowing sluggishly through small pools carpeted with fine mud. Vegetation is scanty and limited to clumps of submerged grass (*Glyceria fluitans*), but actually at the confluence with the Rheidol *Ranunculus aquatilis* grows in profusion. At this station all collecting was performed above a point 10 yards above the confluence.

B. At Capel Bangor. Here the river is steady in flow, its bed being flat and evenly covered with large weathered pebbles and stones. The vegetation

is limited to small and occasional clumps of *Callitriche aquatica* and *Fontinalis antipyretica*. The river is about 12 ft. wide and fringed by the grasses of the neighbouring pastures.

C. Here the water of the river has been partially diverted through a mill race to work a water wheel used to generate electricity. The mill race channel measures about 6 ft. in width by 1–2 ft. in depth, and its bed is composed of fine sand and mud and is covered with accumulations of dead leaves and other debris. There is a profusion of aquatic vegetation, including great masses of *Callitriche aquatica*, *Glyceria fluitans*, and *Lemna minor*. After working the water wheel the stream returns to its normal course. At this station the fauna of the mill race channel and the mainstream immediately above its origin was investigated.

D. and E. Here the river is swift and steady in flow and about 6 ft. wide. The bed is stony and the vegetation limited to the pasture grasses fringing its margins and very occasional clumps of *Fontinalis antipyretica*.

F. This is the portion of the stream adjoining and immediately below the Goginan Mine dump, and has already been described.

G. Here the stream is 4–6 ft. wide, flowing swiftly over a stony bed and here and there cascading through rocky pools in which there are fine mud deposits. There is an abundant flora, including great masses of *Fontinalis antipyretica*, and the stony bed is covered with a wealth of algal growth.

(*b*) *Method of sampling*

At all stations the following collecting method was employed. Large numbers of the submerged stones were partly raised and gently brushed with the hand so that the animals clinging upon or beneath them were swept by the current into a large canvas water-net of semicircular opening and held immediately downstream. At station F this was the only collecting method which yielded any result. Dead leaves and other debris on the stream bed were stirred up and the animals sheltering therein captured with the net, which was also worked vigorously through all the submerged vegetation encountered. Samples of sand and mud deposits were sieved through a sieve of suitable mesh and the animals retained by the sieve and the entire contents of the net were transferred, with about a litre of water, to a 2-litre collecting jar. All material collected was carefully examined at the laboratory, where the various species were sorted out, counted and identified.

At each collecting station the section of the river studied measured approximately 150 yards in length. Approximately three-quarters of an hour was spent in collecting on each occasion.

Two samples of the fauna were taken at each station. The collecting dates, which were suitably "staggered", are given in Table 2.

Table 2. *Species collected in the River Melindwr*

Collecting station ...	A	B	C	D	E	F	G
Dates (1939) ...	16 June 29 June	27 May 9 June	29 May 6 June	11 June 21 June	17 June 24 June	18 June 27 June	10 June 25 June
PLATYHELMINTHES							
Polycelis nigra Müll.	1	6	19	5	—	—	—
P. cornuta (Johnson)	2	4	5	14	—	—	—
Planaria alpina (Dana)	2	8	—	3	14	—	21
OLIGOCHAETA sp.	6	45	—	—	—	—	3
HIRUDINEA							
Haemopis sanguisuga L.	—	1	1	—	—	—	—
Herpobdella atomaria Carena	—	2	—	—	—	—	—
MOLLUSCA							
Ancylastrum fluviatile Müll.	—	—	—	—	—	—	32
ARACHNIDA							
Hydracarina spp.	38	10	28	4	—	—	4
INSECTA							
Collembola							
Isotoma sp.	—	1	—	—	—	—	—
Plecoptera							
Isopteryx sp.	1	8	4	4	4	22	1
Leuctra sp.	2	3	—	3	1	44	4
Taeniopteryx sp.	—	—	1	—	—	—	—
Perlodes sp.	—	—	1	—	—	—	—
Chloroperla sp.	—	—	1	—	1	—	3
Nemura sp. *a*	—	1	1	1	2	1	—
Nemura sp. *b*	—	—	—	—	2	2	7
Nemura sp. *c*	—	—	2	—	8	—	—
Ephemeroptera							
Baëtis sp.	*N*	*N*	*N*	*N*	*N*	*N*	*N*
Rithrogena sp.	—	12	—	2	42	24	—
Ecdyonurus sp.	—	1	—	1	3	—	13
Siphlonurus sp.	2	—	34	2	—	—	—
Ephemerella sp.	33	22	19	13	27	—	49
Odonata							
Cordulegaster annulatus Latr.	—	1	1	1	3	—	3
Calopteryx virgo L.	—	—	4	—	—	—	—
Hemiptera							
Gerris najas De G.	—	—	2	—	—	—	—
G. gibbifera Schum.	—	1	3	1	1	—	1
G. lacustris L.	1	1	1	—	—	—	—
Velia currens Fab.	*N*	*N*	*N*	*N*	*N*	*N*	*N*
Hydrometra stagnorum L.	—	—	3	—	—	1	—
Corixa sahlbergei Fieb.	1	—	—	—	1	—	—
C. striata Fieb.	2	1	—	—	—	—	—
Corixa sp. *a*	1	—	—	—	2	—	—
Corixa spp. nymphs	35	—	—	—	—	—	—
Trichoptera							
Glossosoma boltoni Curt (bred out)	*N*	*N*	*N*	*N*	*N*	74	*N*
Rhyacophila dorsalis Curt. (bred out)	1	5	—	7	8	8	11
Rhyacophila sp. *a*	—	—	—	—	—	—	3
Hydropsyche spp.	7	4	—	—	14	—	97
Polycentropus flavomaculatus Pict.	3	3	9	6	5	24	7
Plectrocnemia conspersa Curt.	1	—	—	2	—	—	—
Philopotamus montanus Donov. (bred out)	—	—	—	—	—	—	17
Halesus radiatus Curt. (bred out)	12	43	78	92	84	—	39

Table 2 (*continued*)

Collecting station ...	A	B	C	D	E	F	G
Dates (1939) ...	16 June 29 June	27 May 9 June	29 May 6 June	11 June 21 June	17 June 24 June	18 June 27 June	10 June 25 June
TRICHOPTERA (cont.)							
Silo pallipes Fab. (bred out)	*N*	*N*	*N*	*N*	32	3	—
Lepidostoma hirtum Fab. (bred out)	2	1	4	8	3	3	8
Sericostoma personatum Spence (bred out)	17	29	13	29	19	3	18
Stenophylax stellatus Curt. (bred out)	—	—	2	—	—	4	1
Odontocerum albicorne Scop.	—	—	—	2	3	4	2
Anabolia nervosa Leach (bred out)	4	—	—	—	—	—	—
Drusus annulatus Steph.	—	—	—	—	—	—	4
COLEOPTERA (imagines)							
Haliplus lineatocollis Marsh	7	3	10	—	1	—	—
Gyrinus natator L.	8	1	—	—	—	—	—
Orectochilus villosus Müll.	13	—	—	2	—	—	—
Dytiscus marginalis L.	1	—	—	—	—	—	—
Illybius fuliginosus F.	2	1	13	3	—	—	—
Platambus maculatus L.	10	11	1	—	—	—	—
Agabus guttatus Pk.	1	—	—	—	—	—	—
A. strumi Gyll.	—	2	—	—	—	—	—
A. bipustulatus L.	—	3	2	2	2	—	—
A. paludosus F.	6	14	5	5	5	—	—
A. didymus Ol.	4	2	5	—	1	—	—
Deronectes latus Steph.	—	1	—	—	—	—	—
Hygrotus inaequalis F.	—	1	—	—	—	—	—
Oreodytes rivalis Gyll.	1	—	—	—	—	3	—
Hydroporus palustris L.	—	—	8	—	—	—	—
H. lepidus Ol.	—	—	1	1	—	—	—
H. discretus Fair.	—	—	2	—	—	—	—
H. planus F.	—	2	4	—	—	—	—
Hydrobius fuscipes L.	—	1	—	—	—	—	—
Helophorus aquaticus L.	10	2	1	—	—	—	—
Helophorus sp. *a*	49	25	7	4	—	—	—
Anacaena globulus Pk.	—	6	12	—	1	—	—
Limnebius truncatellus Thunb.	—	—	—	2	—	—	—
Laccobius nigriceps Th.	—	3	—	—	1	—	—
Helmis maugei Bed.	—	1	—	1	—	—	2
Latelmis volkmari Pz.	—	—	—	—	—	1	1
Dryops sp.	3	4	6	—	—	—	—
COLEOPTERA (larvae)							
Dytiscus marginalis L.	—	—	1	—	1	—	—
D. semisulcatus Müll.	—	—	—	—	1	3	—
Other Dytiscid larvae	—	—	—	7	3	—	—
Gyrinid larvae	3	—	—	—	—	—	—
DIPTERA							
Chironomus sp.	33	35	23	4	—	—	—
Forcipomyia sp.	—	3	3	4	—	—	—
Tanypus sp.	16	7	14	4	—	—	—
Dixa sp.	6	—	1	2	1	—	16
Simulium sp.	*N*	*N*	17	*N*	*N*	*N*	*N*
Dicranota sp.	—	—	4	—	—	—	3
Tabanus sp.	—	—	—	—	—	3	—
Nematoceran pupae	4	—	1	—	—	—	1
VERTEBRATA							
PISCES							
Gasterosteus aculeatus L.	42	—	—	—	—	—	—
Phoxinus phoxinus (L.)	—	—	—	—	—	—	10*
Salmo trutta L.	—	2*	—	—	—	—	4*
AMPHIBIA							
Bufo b. bufo (L.) (tadpoles)	—	—	*N*	—	4	—	—

* Number of fish captured. More fish were seen.

(*c*) *Faunistic data*

All the animal species recorded are listed in Table 2, which also gives the numbers captured at the various collecting stations. The figures are the total number of individuals taken at the collecting station, i.e. each is a sum total for two samples. Where this exceeded a hundred the symbol *N* (numerous) has been inserted. No attempt was made to collect and identify Protozoa, Rotifera and Nematoda, so that, strictly speaking, Table 2 lists the macrofauna only.

The works consulted for the identification of the specimens are listed in Laurie & Jones, 1938, and some additional ones at the end of the present paper. For assistance in the identification of the Coleoptera the writer wishes to thank Prof. F. Balfour-Browne, who confirmed the identification of sample specimens of all the Adephagid and Hydrophilid species (imagines) recorded. For assistance in the identification of the Trichopteran larvae the writer thanks Mr Harry Evans of the Department of Zoology at Aberystwyth, who has specifically identified a number of the Trichopteran larvae of the Aberystwyth district by rearing them to the adult stage. The identification of the imagines reared has been confirmed by Messrs M. E. Mosely and D. E. Kimmins.

Specimens of nearly all the species recorded have been preserved, and form part of the Freshwater Fauna collection of the Department of Zoology at Aberystwyth.

5. Discussion

Table 2 shows that the river carries a reasonably rich and varied fauna. Above the sources of pollution minnows and trout occur in fair numbers; at stations C, D, E and F no fish were seen or captured, but in the small pools near the confluence with the Rheidol sticklebacks are abundant, while trout were seen and captured at station B. The sticklebacks do not seem to venture farther up the river, and in all probability the trout occurring in its polluted lower reaches are visitors from the Rheidol. This is not surprising, since the dissolved lead content of the river frequently reaches a level fatal to fish. Thus the writer (1938*a*) has shown that the maximum concentration of dissolved lead in soft water that the stickleback can withstand is approximately 0·1 mg. Pb per litre, and it is very probable that the sensitivity of the trout is of the same order.

Carpenter has classed the Mollusca with the fishes as animals highly sensitive to the toxic action of dissolved lead salts; thus Carpenter (1926, p. 397) writes: "the disappearance of Mollusca is the first index to the pollution of a stream by lead mining." This conclusion is endorsed by the writer's study of the Melindwr. No Mollusca occur below the sources of pollution, though *Ancylastrum fluviatile* occurs in fair numbers in the upper unpolluted reaches. A check examination on 5 July 1939 showed that *Ancylastrum* could be found on most of the stones on the stream bed immediately above the confluence with

the Nant Brwyno, while a thorough search below this point failed to reveal a single specimen. *Ancylastrum*, *Limnaea peregra* and a species of *Pisidium* are abundant in the lower reaches of the Rheidol, while a small weedy ditch joining the Melindwr some distance above its confluence with the Rheidol also contains numbers of *L. peregra*. Experimental evidence of the sensitivity of Mollusca to the toxic action of lead salts is somewhat lacking, though the writer (1938*b*) has shown that a 3 mg. per litre solution of lead is fatal to *Limnaea* in 4 hr. and to *Ancylastrum* in 15 hr.

Hirudinea are very rare in the lower reaches of the Melindwr, but appear completely absent above, and so their rarity in the polluted reaches cannot be regarded as significant. Planarians are reasonably numerous at all parts of the river except the silted area adjoining the mine dump. The effect of dissolved lead salts upon these animals requires further investigation; Carpenter (1924) has stated that planarians are completely absent from streams seriously polluted by lead-mine effluents, but the writer (1938*b*) finds that *Polycelis nigra* survives for 70 days in a lead-nitrate solution containing 3 mg. Pb per litre.

It will be noted that the fauna of the silted area adjoining the mine dump is rigidly limited to insects, not a single specimen of any other animal group occurring at this station. Among insects Carpenter singled out the Trichoptera as the order most sensitive to the toxic effect of lead-mine effluents; thus Carpenter (1924, p. 14) records that before May 1922 no Trichoptera were represented in the fauna of the Rheidol, then heavily lead polluted, but that eight species of this order subsequently became established when the degree of pollution sensibly diminished. And she states (1926) that Trichopteran larvae do not become re-established in streams recovering from pollution by lead-mine effluents until the pollution has become intermittent, the supply of soluble lead being renewed at flood time only.

The distribution of the Trichopteran larvae in the Melindwr exhibits certain features of interest. In particular, at the silted area adjoining the mine dump the portable case-carrying species are markedly less abundant than at the other stations. Thus the larva of *Halesus radiatus*, the most common of the large case-carrying larvae of the river, occurs in considerable numbers below and above the lead mine, but at the silted area near the dump not a single specimen was found. *Sericostoma personatum* is considerably less numerous here than at other stations. *Silo pallipes* is numerous at all stations below the mine, whereas the two collections in the immediate vicinity of the mine revealed three specimens only. This species, however, does not reappear above the sources of pollution. The distribution of these Trichopteran species was checked by careful re-examinations at all the collecting stations on 2 and 7 July 1939, the results of which confirmed previous observations.

The complete absence of *Halesus* from station F is somewhat significant. The larva carries a very untidy case which is usually constructed entirely from vegetable material, including pieces of leaves, plant stems and small sticks

(Fig. 1*a*). It has been noted that adjoining the mine dump the river is devoid of vegetation and this might appear to suggest that the larva's absence from this area can be attributed to the lack of suitable material wherewith to build its case. That many Trichopteran larvae display considerable elasticity in their selection of materials for case building is well known; experiments were therefore made to ascertain whether *Halesus* larvae could build cases with the mine-dump material. Six larvae of various sizes, ejected from their normal cases, were placed in a small aquarium containing no plant material and supplied with a quantity of washed grit from the mine dump. Three of the larvae rapidly constructed cases, one of which is illustrated in Fig. 1*b*. A number of *Halesus* larvae captured at station E, where vegetation is extremely scanty, were found to have cases mainly composed of lead-mine grit, together with small quantities of vegetable material; a typical example is illustrated in Fig. 1*c*. Above the lead mine *Halesus* again occurs in numbers, building its usual case of vegetable material exclusively.

Similar experiments proved that *Silo pallipes* and *Sericostoma personatum* could also build cases entirely composed of the gritty mine-dump material. Young larvae proved to be more successful at case construction than those more mature. Cases built by *Silo* and *Sericostoma* are illustrated in Fig. 1*e*, *g*. The scarcity of *Halesus*, *Silo* and *Sericostoma* at the mine-dump station, therefore does not appear to be due to inability to find materials for case building; nor can it be attributed to the dissolved lead content of the water. No tributaries enter the stream between stations F and D, so that the dissolved lead content cannot diminish appreciably by the time the water reaches the latter station. Here the stream harbours large numbers of the Trichopteran species which apparently find it difficult or impossible to exist at station F.

There remains the question of the available food material. Slack (1936) has shown that the larva of *Silo nigricornis* is a typical diatom feeder, the gut of these larvae generally being filled with algae of the families Centricae and Pennatae. *Sericostoma personatum* was shown to subsist chiefly on algae and leaf material, though some specimens contained animal food. *Halesus* larvae, according to Slack, have a similar diet of leaves and various algae, two larvae only, out of twenty examined, contained portions of insects. Thus there is good evidence that the Trichopteran species which find it difficult or impossible to maintain an existence at station F are predominatingly phytophagous. That no phanerogams grow in this part of the river has already been noted. Furthermore, it has been shown by Reese (1937) that at this point the river is devoid of microflora. Above and below the stretch carpeted with the mine-dump material the stony stream bed supports a rich and varied microflora; but the grit-covered stones near the mine were found to be completely devoid of vegetation. Miss Reese concludes that the absence of microflora from this portion of the river can be attributed to the scouring and smothering action of the gritty mine refuse material covering the stream bed. It therefore appears

very probable that the scarcity or absence of certain Trichopteran species at station F can be attributed to the lack of suitable food material. The carnivorous Trichopterans *Rhyacophila dorsalis* and *Polycentropus flavomaculatus* are fairly numerous at this station: apparently a sufficiency of animal food is available for them. Four specimens of *Odontocerum albicorne* were also found at station F. Slack (1936) states that this species is largely carnivorous, feeding on algae and a number of insects, including *Baëtis* and Trichopteran larvae. The latter were mainly Polycentropidae.

With the notable exception of the ubiquitous *Velia*, Hemiptera are scarce at all parts of the river. Plecoptera of the genera *Leuctra* and *Isopteryx* are much more abundant at the mine-dump station than elsewhere; possibly they flourish here as a result of the absence of many of their natural enemies.

The general conclusion is that, despite the pollution, a reasonably rich fauna exists at all parts of the river, except the stretch heavily polluted with solid dump material. Here insects alone are able to survive, and the complete absence of vegetation appears to limit the fauna to carnivorous types and types, such as *Simulium*, feeding on food materials brought along by the current. Improvement in the fauna of the lower reaches of the river will probably be a very slow process. The river is comparatively small; the Goginan mine dump is very extensive and doubtless contains vast reserves of potentially soluble lead. Though an abundance of suitable fish food exists at the present time, it is probable that many years will pass before the dissolved lead content of the river falls sufficiently for fish to become numerous and permanent residents.

6. Summary

1. The lower reaches of the river Melindwr, a tributary of the river Rheidol in north Cardiganshire, are polluted with dissolved lead salts carried into the river by water draining the mine dump of the disused lead mine at Goginan. The dissolved lead content of the polluted reaches varies from a trace to 0·3 mg. per litre. Where the river skirts the mine dump, and for a short distance beyond, its bed is thickly carpeted with the gritty mine-dump material.

2. The fauna of the river has been sampled at one station above the sources

Legend to Fig. 1

Fig. 1. (*a*) Larva of *Halesus radiatus* with normal case built entirely from plant materials. (*b*) Larva of *Halesus* with case constructed in the laboratory from mine-dump material. (*c*) *Halesus* larva taken at station E, with case constructed partly from mine-dump gravel and partly from vegetable materials. (*d*) Larva of *Silo pallipes* with normal case of smooth gravel and pebbles. (*e*) Larva of *Silo pallipes* with case constructed in the laboratory from mine-dump material. (*f*) larva of *Sericostoma personatum* with normal case built from smooth sand grains. (*g*) With case built in the laboratory from mine-dump material.

(*a*), (*b*), (*c*), (*f*) and (*g*) × 5, (*d*) and (*e*) × 7·5.

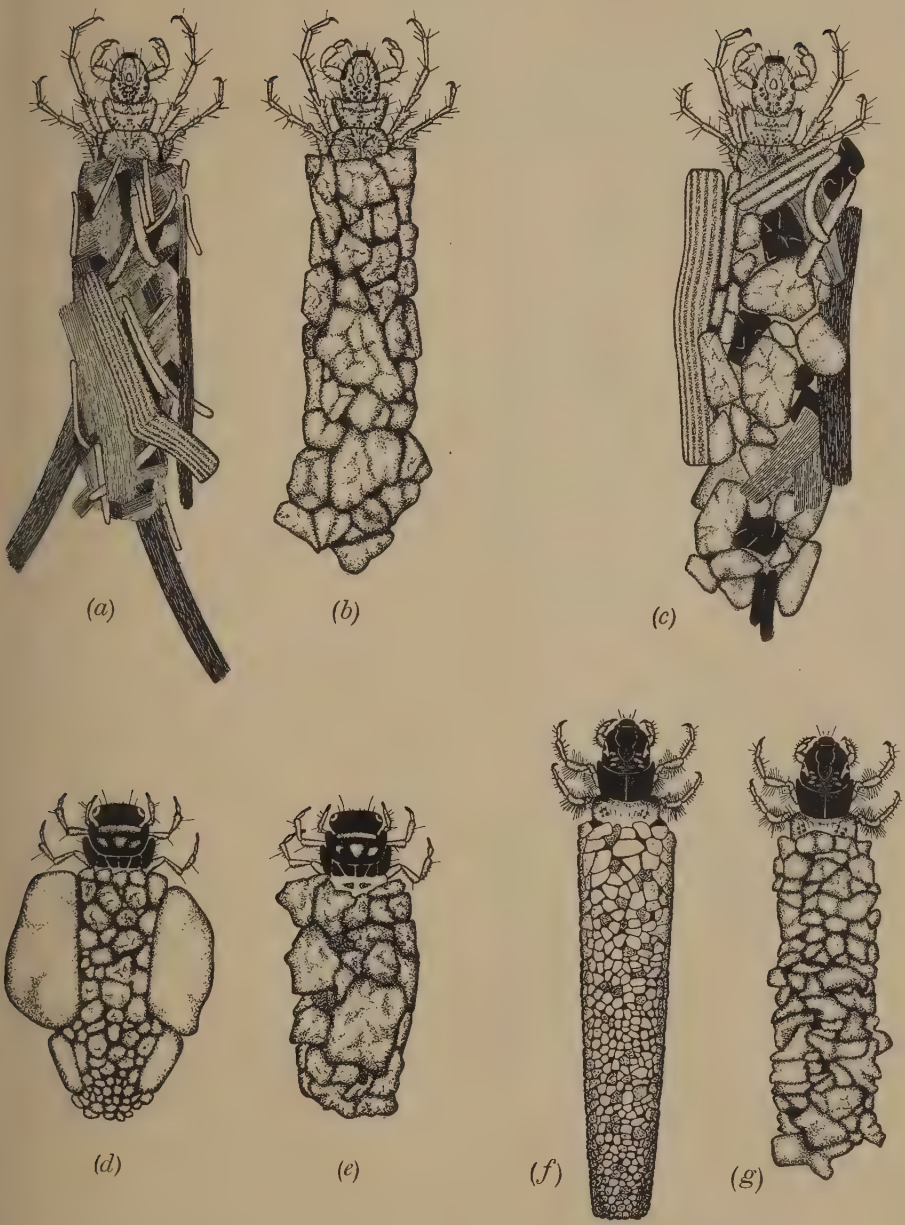

Fig. 1.

of pollution and at six stations along the polluted stretch. Eighty-eight animal species were recorded, seventy-six being insects.

3. Minnows (*Phoxinus phoxinus*) and trout (*Salmo trutta*) occur above the sources of pollution. Sticklebacks (*Gasterosteus aculeatus*) are abundant near the confluence with the Rheidol, but do not seem to venture further up the river. Trout were seen and captured near the confluence; these are probably visitors from the Rheidol.

4. *Ancylastrum fluviatile* occurs in numbers above the sources of pollution; no Mollusca occur below.

5. The fauna of the portion of the river adjoining the mine and heavily polluted with the solid mine-dump material comprises insect species only. Certain case-carrying Trichopteran larvae are absent at this station or much less numerous than at other stations. Their absence or scarcity does not appear to be due to the lead content of the water or to the lack of materials for case building, but to the absence of vegetable food material. No vegetation grows in this part of the river, and the stony stream bed, covered with the mine-dump material supports no microflora (Reese, 1937). Carnivorous Trichopteran larvae, however, are fairly numerous at this station.

6. Improvement in the condition of the river will probably be slow; as the river is small, whereas the mine dump is of great size and probably contains enormous reserves of potentially soluble lead.

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STUDIES OF FLUCTUATIONS IN INSECT POPULATIONS

VII. THE BUTTON TOP MIDGE (*RHABDOPHAGA HETEROBIA*) AT SYSTON, 1934–39

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(*With 4 Figures in the Text*)

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1. Introduction

This is the seventh of a series of papers giving the results of an attempt to study fluctuations in insect populations as they occur in nature. The first five of these studies, all of which were concerned with various species of gall midges, have been discussed in the sixth of the series (**2**) and another paper (**3**).

The present contribution is a continuation of the account, started in the third paper of the series (**1**), of the "button-top" midge, *Rhabdophaga heterobia* H.Lw. (Diptera, Cecidomyidae), on *Salix triandra* variety Black Maul at Syston, Leicestershire. That paper covered the years 1928–33, while the present one deals with 1934–9. In the last section the results of the whole twelve-year period have been discussed. The present paper should be read in conjunction with the general account of the pests on the willows at Syston which was written by Roebuck (**4**), together with the third (**1**) and sixth (**2**) papers in the present series.

The methods used have been the same as in the previous years. The standard size of sample throughout has been 500 galls.

Unfortunately, the particular field of willows, from which the material has been collected each year, has been allowed to go out of cultivation since 1936. The method of eradicating the willows has been to cut down the annual growth at the end of each winter and then allow horses and cattle to graze during the summer. These animals have kept on eating the willow shoots with the result that the annual growth has become less and less until, in the autumn of 1938, the relatively few willows that had survived such treatment were scarcely alive

and the year's growth only a foot or so in height. "Button" galls, however, were still present on almost 100% of the shoots, but they were noticeably small. By the autumn of 1939 the willows had for all practical purposes been exterminated and the field study perforce had to be drawn to a conclusion.

2. Size of population of *Rhabdophaga heterobia* and its parasites, 1934–9

The average numbers of the gall midge and its parasites reared are expressed diagrammatically in Fig. 1. Table 1 gives the numbers of midges and Hymenopterous parasites reared over the period of 1934–9. Both this figure and table are continuations of the corresponding figure (Fig. 1) and table (Table 4) in the third paper of this series (**1**). The figure for the year in each case denotes the year in which the insects emerged: the samples were collected the previous

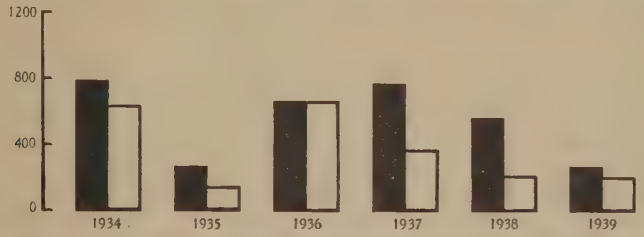

Fig. 1. Average numbers of *Rhabdophaga heterobia* (solid) and parasites (open) emerging from 500 galls, 1934–9.

autumn between 30 October and 2 November. Sample IV, from which insects emerged in 1936, is the exception. This sample was collected on 24 January 1936, whereas the other three samples emerging that year were collected at the normal time the previous year, i.e. 30 October.

This late collection of material was made in order to compare the population of the galls present in January with that of galls present at the end of October. What effect would the winter and consequent hunting for food by birds have had on the insect population? As soon as the field was visited in January, it was obvious that birds had been diligent in eating out many of the larger and more obvious galls. In fact it was difficult to find any of normal size, those remaining being all undersized as compared with those of the previous October. Table 1 shows that the total insect population was slightly over 900 compared with 1200–1500 of the samples collected before the winter months. Both the numbers of the midges and parasites, as to be expected, were reduced considerably. In other respects, i.e. dates and crests of emergence of host midge and its parasites (D, Table 3) sex ratio of the midge and relative parasitism, the samples collected in October and January did not appreciably differ.

The successive reduction in total insect population from 1933 (average 3238 midges and parasites) to 1934 (average 1429 midges and parasites) and to

1935 (average 382 midges and parasites) may have been due, partially at any rate, to the effect of the comparatively dry hot summers of 1933 and 1934 and the consequent diminution of luxuriant willow growth. It must be remembered that only the overwintering generation of midges and parasites was studied, and so the 1934 population recorded would be that which developed in the late summer of 1933. In 1936, i.e. after the summer conditions of 1935, the population had risen again to an average total of 1350, still less than half the 3000 estimated (**1**) normal insect population for 500 galls. In 1937 the effect of allowing the willows to go out of cultivation prevented any further return to the normal and, subsequently, in 1938 and 1939 this effect was overwhelming, the average population dropping from 1129 in 1937 to 786 and 742 in 1938 and 1939 respectively.

Table 1. *Population of* 500 *galls of* Rhabdophaga heterobia, 1934–9

Year	Total midges	Sex ratio	Total Hymenopterous parasites	Parasitism %	Total insects
1934 (i)	876	44 : 56	566	39	1442
(ii)	858	43 : 57	647	43	1505
(iii)	655	49 : 51	687	51	1342
1935 (i)	245	41 : 59	147	37·5	392
(ii)	253	40 : 60	158	38	411
(iii)	203	35 : 65	139	40	342
1936 (i)	637	43 : 57	601	48·5	1238
(ii)	590	49 : 51	671	53	1261
(iii)	799	45 : 55	751	48	1550
*(iv)	416	44 : 56	520	55·5	936
1937 (i)	790	41 : 59	288	27	1078
(ii)	788	43 : 57	410	34	1198
(iii)	772	41 : 59	340	31	1112
1938 (i)	566	39 : 61	191	25	757
(ii)	543	41 : 59	226	29	769
(iii)	614	48 : 52	219	26	833
1939 (i)	261	44 : 56	207	44	468
(ii)	216	34 : 66	222	51	437
(iii)	320	43 : 57	191	37	511

* Galls collected on 24 January 1936.

The sex ratio of the midge during the period under consideration varied from 34 : 66 to 49 : 51 which closely resembled the range (35 : 65 to 48 : 52) during the previous six years. There was no evidence that the numbers of males decreased as the total midge population increased as had been previously suggested.

Three further examples of hermaphrodite individuals have been reared; one in 1934 which had male antennae but possessed an ovipositor, one in 1936 with female antennae and male genitalia and one in 1938 also with female antennae and male genitalia. Out of about 30,000 midges reared in the 12 years, there have been only 5 such individuals, of which four had female antennae and male genitalia.

3. Relative parasitism of the midge

The parasites involved comprise six species (**1**). All the parasites reared during the twelve years, 1928–39, have been retained; those emerging in the seven years 1928–32 and 1938–9 have been kept according to which sample they belonged irrespective of their dates of emergence, while those emerging during the five years 1933–7 have been kept according to the dates of emergence irrespective of the particular sample from which they emerged. A start has

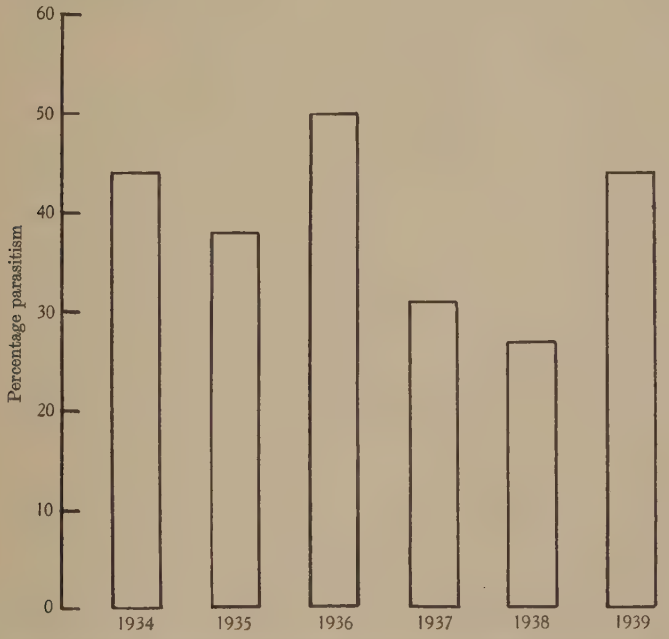

Fig. 2. Average relative parasitism of overwintering generation of *Rhabdophaga heterobia*, 1934–9.

been made in studying the numerical interrelationships of the various species and their seasonal emergence, and it is hoped to publish the results in due course, and so conclude this study of *R. heterobia* and its parasites.

Meanwhile, the gross relative parasitism in the separate samples can be seen in Table 1, and the average yearly relative parasitism of the midge is set out graphically in Fig. 2. This figure is the continuation of the corresponding figure (Fig. 2) in the previous paper (**1**). On the whole, the degree of parasitism has been less than in the previous six years, excluding the peculiar year 1933. Although the average total numbers of midges and parasites fell from 3238 in 1933 to 1429 in 1934 and to 382 in 1935 (Table 4) the average relative parasitism did not depart very appreciably from the 50% level. This would support

the suggestion made in the previous section that the reduction in total population was perhaps due to the effect of the summers of 1933 and 1934 on the willows' growth. From 1936 to 1938 there was a decrease in relative parasitism. This decline is probably partially due to the effect of the willows being allowed to go out of cultivation, although the rise in relative parasitism in 1939 would seem to indicate that the availability of midges as food for the parasite complex plays a not inconsiderable part (Fig. 3).

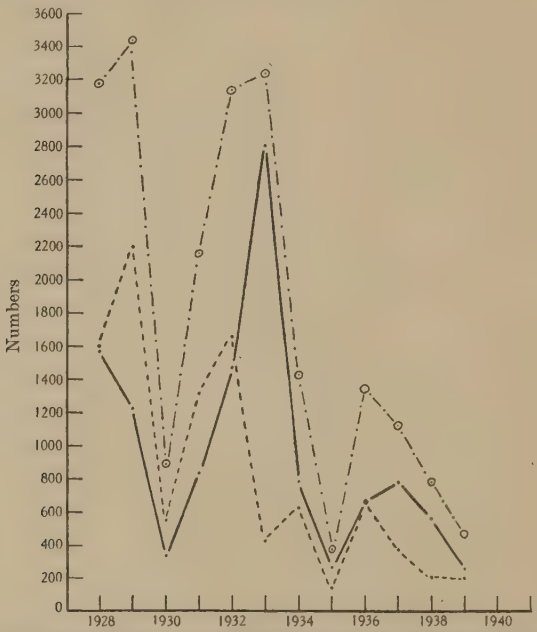

Fig. 3. Average total numbers of *Rhabdophaga heterobia* plus its parasites (-·-·-); average numbers of gall midges alone (—) and of parasites alone (---); for years 1928–39.

4. Emergence

Table 2 (compare Table 5 in (**1**)) shows the dates of the actual first emergence, the peak of emergence, the number of days to reach the peak and the date of the last emergence of *R. heterobia* in the samples as kept in the unheated insectary during the period 1934–39 inclusive.

The range of first emergence was from 13 April to 12 May (29 days), while that of the peaks is from 19 May to 5 June (17 days). Within samples of the same year the corresponding range between dates of first emergences has been 4 days in 1935 and 1939, 3 in 1934, 2 in 1937 and 1 day in 1936 and 1938. In the last-named year in samples (ii) and (iii) only single individuals emerged on 13 and 28 April and emergence did not start again till 4 and 5 May. The

time which lapsed between the first emergence and the peak varies from 10 to 32 days if one ignores the second sample of 1939 for the reason given above. The variation within any one year is less, 14–15 days in 1936, 22–24 days in 1937, 21–25 days in 1939, 23–30 days in 1935, 22 -32 days in 1938 and 10–24 days in 1934.

Table 2. *Dates of actual first emergence, peak of emergence, number of days to reach peak and the dates of the last emergences of* Rhabdophaga heterobia, 1934–9

Year	Date of first emergence	Date of peak of emergence	Days to reach the peak	Date of last emergence
1934 (i)	9 May	19 May	10	1 July
(ii)	10 May	3 June	24	3 July
(iii)	12 May	23 May	11	4 July
1935 (i)	5 May	30 May	25	9 July
(ii)	7 May	30 May	23	5 July
(iii)	3 May	2 June	30	5 July
1936 (i)	5 May	19 May	14	1 July
(ii)	4 May	19 May	15	27 June
(iii)	5 May	19 May	14	30 June
1937 (i)	7 May	29 May	22	13 July
(ii)	5 May	29 May	24	7 July
(iii)	5 May	29 May	24	5 July
1938 (i)	4 May	5 June	32	20 July
(ii)	13 April*	5 June	53 (32)	29 June
(iii)	28 April*	27 May	29 (22)	6 July
1939 (i)	7 May	30 May	23	19 July
(ii)	6 May	31 May	25	9 July
(iii)	10 May	31 May	21	10 July

* Single individuals, then (ii) restarted on 4 May and (iii) on 5 May.

The actual peak day of emergence, however, is not so reliable as the week in which the maximum numbers of midges (or parasites) emerged. The dates and figures in Table 3 (corresponds to Table 6 in (**1**)) shows the weekly emergences of the midge and its parasites. The top row of figures in each case refers to the midge, while the lower row refers to the parasites. The peaks are in heavy type. It will be seen that a weekly crest of emergence of the midge has occurred three times in the week 14–20 May, four times in the week 21–27 May, ten times in the week 28 May–3 June and twice in the week 4–10 June. However, these latter two occurrences might well have been in the week 21–27 May. In the three samples of any one year the peak has occurred two years in the same week, three years within a fortnight and one year in a period of three weeks.

The peak emergence of the parasites has occurred three times in the week 28 May to 3 June, nine times in the week 4–10 June, three times in the week 11–17 June and three times in the week 25 June to 1 July. As in the previous study, no variation occurred within the samples of any one year. Usually the peak week of emergence of parasites occurred in the first to fourth week after that of its host midge; but in 1937 and 1938 the weekly peak of the parasite was the same as that of the midges in five out of six samples.

Table 3. *Weekly emergence of* Rhabdophaga heterobia *and its parasites*, 1934–9. *The upper rows of figures refer to the midges while the lower refer to the parasites. The figures in heavy type indicate the peak weeks*

Year	Date and size of sample	23–29 April	30 April–6 May	7–13 May	14–20 May	21–27 May	28 May–3 June	4–10 June	11–17 June	18–24 June	25 June–1 July	2–8 July	9–15 July	16–22 July	July–August later	Total host and parasites	Parasitism %
1934	31 Oct. 1933, 500 galls, A	—	—	73	153	270	**273**	76	22	4	5	—	—	—	—	876	39
				1	0	12	102	154	**203**	63	18	10	2	1	—	566	
	B	—	—	20	84	239	**314**	110	65	17	8	1	—	—	—	858	43
					2	23	91	182	**246**	72	14	17	—	—	—	647	
	C	—	—	9	61	**239**	193	73	41	18	14	7	—	—	—	655	51
						15	141	196	**227**	71	20	10	6	0	1	687	
1935	1 Nov. 1934, 500 galls, A	—	3	14	19	56	**56**	31	23	14	27	1	1	—	—	245	37·5
					1	2	8	8	15	37	**42**	27	7	—	—	147	
	B	—	—	15	17	54	**68**	60	20	7	11	1	—	—	—	253	38
						4	12	16	17	42	**48**	16	2	1	—	158	
	C	—	4	8	5	34	**42**	37	29	19	21	3	1	—	—	203	40
								2	10	36	**65**	13	10	3	—	139	
1936	30 Oct. 1935, 500 galls, A	—	1	3	193	**211**	103	92	16	13	5	—	—	—	—	637	48·5
					19	67	81	**190**	144	98	2	—	—	—	—	601	
	B	—	2	10	**230**	139	68	104	28	8	1	—	—	—	—	590	53
					25	103	125	**212**	129	74	2	1	—	—	—	671	
	C	—	1	17	**248**	216	103	140	61	12	1	—	—	—	—	799	48
					31	102	117	**223**	187	87	3	1	—	—	—	751	
	24 Jan. 1936, 500 galls, D	—	—	4	**159**	101	54	66	15	16	1	—	—	—	—	416	55·5
					6	40	72	**172**	155	72	1	1	—	—	—	520	
1937	30 Oct. 1936, 500 galls, A	—	—	3	32	180	**289**	217	42	14	10	2	1	—	—	790	27
						30	**120**	63	47	17	9	2	—	—	—	288	
	B	—	1	9	36	195	**301**	170	55	11	6	4	—	—	—	788	34
						41	**166**	118	45	27	11	2	—	—	—	410	
	C	—	4	7	42	213	**319**	138	26	13	9	1	—	—	—	772	31
						29	**153**	97	33	12	15	1	—	—	—	340	
1938	2 Nov. 1937, 500 galls, A	—	2	20	90	156	75	**161**	45	13	3	0	0	1	—	566	25
					3	33	32	**64**	35	20	0	2	0	2	—	191	
	B	1	3	29	82	135	113	**143**	27	6	4	—	—	—	—	543	29
		(13 April)			6	26	42	**80**	40	24	7	0	0	1	—	226	
	C	1	2	7	96	**175**	121	148	49	8	4	3	—	—	—	614	26
					3	17	27	**58**	57	45	10	2	—	—	—	219	
1939	31 Oct. 1938, 500 galls, A	—	—	8	14	**93**	82	37	12	5	5	3	1	1	—	261	44
						9	52	**105**	25	12	3	1	—	—	—	207	
	B	—	1	5	4	53	**69**	47	16	6	12	2	1	—	—	216	51
					1	18	53	**94**	38	13	1	3	0	1	—	222	
	C	—	—	8	19	87	**121**	56	12	4	5	6	2	—	—	320	37
						5	49	**91**	28	14	3	1	—	—	—	191	

An additional sample of 500 galls collected on 1 November 1935 was placed in a warm glasshouse on 5 March 1936 after being previously kept in the usual unheated insectary. The midges and parasites quickly responded to the extra warmth. The former started emerging on 19 March compared with 4 May in the samples kept continuously in the insectary. The parasites started on 23 March as compared with 15 May. The crest of emergence of the midges was on 3 April. The emergences of midges ended on 1 May, while that of the parasites ended on 30 April. The duration of the emergences was distinctly shorter than under the insectary conditions of normal outside varying temperatures. Under these conditions of extra heat in the spring the duration of midge emergence was 43 days compared with 57, 54 and 56 days under normal conditions. The crest was reached after the same number of days, under the extra heat (15 days) and under normal temperatures 14, 15 and 14 days) (see Table 2). Slightly fewer midges and parasites (475 and 595) emerged under these glasshouse conditions than under the usual insectary ones (637, 590, 799 midges and 601, 671 and 751 parasites). The parasitism (55·6%) and the sex ratio (46 : 54) showed no appreciable difference.

5. Discussion of results, 1928–39

The particular field (planted in 1918) in which the galls were collected each year was chosen because it formed part of an old willow bed (established for over 40 years). Ample time should have lapsed since its original planting for the button-top midge and all its parasites and predators to have arrived and become firmly established. It has already been pointed out (**2**) that the weather may react directly on the host insect (*R. heterobia*) or indirectly on it through its effect on the host plant or on the insect's parasites and other enemies.

It is convenient to consider the results under three headings, viz. (*a*) the insect population (i.e. the host gall midge and its parasites) of 500 galls, (*b*) the relative parasitism of the midge (i.e. the proportion of parasites –midges emerging) and (*c*) the emergence of the gall midge. A discussion of the emergence of its parasites and the relative numbers of the various species involved must be left to a further paper.

It must be remembered throughout that only the overwintering generation, i.e. every third, was studied.

(*a*) *Insect population of* 500 *galls*

Fig. 3 shows graphically the average total numbers of the gall midge and its parasites (i.e. the total number of midges if there had been no parasitism), the average totals of the gall midge alone and the average totals of all its parasites considered together for the whole period under discussion. Table 4 gives the details and the average relative parasitism in addition. In four years (1928, 1929, 1932 and 1933) the total insect population was slightly over 3000.

It is thought that under ordinary good conditions of plant growth this figure represents the insect population that can be maintained in 500 galls. This number is not the number which would normally reach the adult state owing to the fact that various birds, especially tits, raid the galls during the winter months. The extent of this reduction in population can be judged by the figures given in Table 1 for the sample (D) collected in late January compared with those (A, B, C) collected at the end of the previous October. It must be remembered in this connexion, however, that tits when marauding the galls drop a considerable portion of each gall to the ground and doubtless some insects could be found in these bits. They would certainly be able to come to maturity on the ground.

Table 4. *Average numbers of midges, parasites and total insects in* 500 *galls*, 1928–39

Year	Midges	Parasites	Total insects	% parasitism
1928	1573	1607	3180	51
1929	1235	2204	3439	64
1930	341	556	897	62
1931	840	1323	2163	61
1932	1480	1662	3142	53
1933	2810	428	3238	13
1934	796	633	1429	44
1935	234	148	382	38
1936	675	674	1349	50
1937	783	346	1129	31
1938	574	212	786	27
1939	265	207	472	44

In 1930 and also in 1934 and 1935 the total insect population showed remarkable drops. It has already been suggested (**1**) that the 1930 decrease was due to the effect of the August-September 1929 drought on the behaviour of the sap in the willows. The sap stopped rising, thus cutting the food supply of the insects about to overwinter, and the winter buds were formed very early. In a similar manner the hot dry summers of 1933 and 1934 may have been responsible for the fall in insect numbers in 1934 and 1935 through their effect on plant growth. In the first instance, the willows and the insect population took two seasons 1930 and 1931 (or six generations of midge) to recover their normal growth and numbers, the latter in the spring of 1932.

In the second instance the 1936 figures showed an increase over the 1935 figures, but further recovery to normality was prevented by the fact that by this date the willows were being allowed to go out of cultivation and be exterminated by cattle. From this date onwards the insect population steadily decreased for the same reason.

(*b*) *Relative parasitism of the midge*

In addition to the six species of parasitic Hymenoptera that have been reared, a predaceous Cecidomyid, *Lestodiplosis* sp., has been reared in insignificant numbers as follows: 1928, 3; 1929, 18; 1930, 12; 1931, 3; 1932, 3; 1933, 4; 1934, 11; 1935, 1; 1936, nil; 1937, 1; 1938, nil; 1939, 2.

Reference to Table 4 and Fig. 3 shows that there exists a positive correlation between the numbers of midges and parasites. This suggests that relative parasitism as high as 64% exerts no control on the numbers of midges. There is no correlation between the size of total population (midges and parasites) and the percentage parasitism. Additional examination of the data involving the percentage changes from year to year in the numbers of the total population and in those of the parasites reveals that such changes are almost identical (regression of log of parasites on log of total population equals +0·9). This indicates that the parasites do not become any more efficient at high populations than at low ones and therefore cannot have any balancing effect by cutting off extreme fluctuations.

There is no evidence that the absolute number of parasites lags behind that of the host midge. This may be due to the fact that only every third generation was studied.

Fig. 3 also shows clearly that when the numbers of midges dropped in 1930 and again in 1935, the numbers of parasites also dropped, while the relative parasitism was hardly affected.

On the other hand, the relative parasitism in 1933 was exceptionally low, although the numbers of midges was high. It has previously been suggested (**2**) that a reversal in the relative times of emergence of host insect and parasites is a possible explanation of this sudden fall in numbers of parasites.

(*c*) *Emergence*

Table 5 shows the frequency of the weekly period of peak emergence of *R. heterobia* and its parasites, collected at Syston in the autumn and kept over the winter at Harpenden, during the twelve years under consideration. It will be seen that usually most of the midges emerged in the week 28 May to 3 June, while most of the parasites emerged within the subsequent two weeks. The details of the actual numbers of midges emerging have been given in Table 3 of the present paper and Table 6 of (**1**).

Table 5. *Frequency of peak emergence of* R. heterobia *and its parasites*, 1928–39

	Occurrences	
Week	Midge	Parasites
14–20 May	2	—
21–27 May	9	—
28 May–3 June	15	3
4–10 June	3	12
11–17 June	3	11
18–24 June	—	3
25 June–1 July	—	3

Fig. 4 gives the dates of first emergence of the midge and its parasites during the twelve years as well as the peak weeks. The full lines represent the midge, while the dotted lines represent the parasites. The horizontal lines

represent the weeks of the peak emergences. It will be seen that the seasonal effect on the first dates of midge emergence is large, the range of first emergence extending from 13 April to 16 May. But the peak week of midge emergence, i.e. the week in which the greatest numbers of the midges emerge, is fairly constant. In the case of the first emergences the parasites[1] are not so affected as the midges, but the peak weeks of the parasites are more variable than those of the midges. This is probably due to variations from year to year in the numbers of individuals in the six species of parasites involved and the seasonal dates of emergence of the species. The first dates of emergence do not appear to be such reliable indicators of the season's earliness or lateness as are the peak weeks of emergence. But it must be remembered that "earliness" or "lateness" alters very rapidly even from week to week in some seasons.

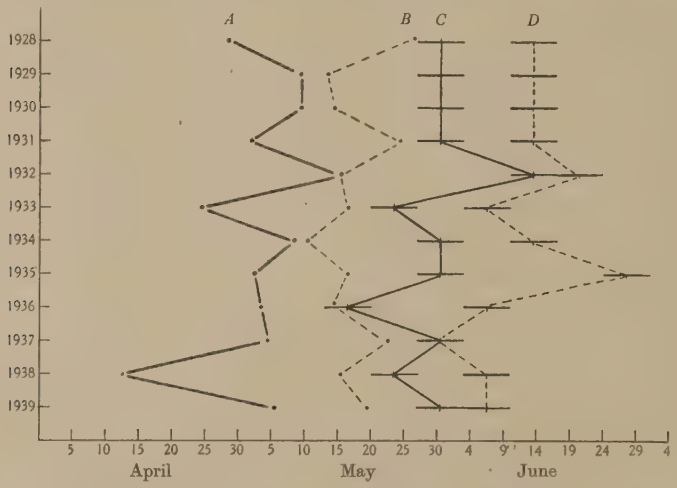

Fig. 4. First and peak weeks of emergence of *Rhabdophaga heterobia* and its parasites, 1928–39. *A*, 1st emergence of *R. heterobia*; *B*, that of parasites; *C*, peak week of *R. heterobia*; and *D*, that of parasites.

The view is put forward that the graphs indicate that although the weather usually affects the midge and its parasites to the same extent, it does not invariably do so. If this is the case one can see how in some years, although the parasites are abundant, they will not be able to attack successfully the midges owing to the different relative periods of emergence.

In conclusion, this twelve year study has served to illustrate the immense complexity of populations in the field and the almost insuperable difficulties encountered when studying them. However, this type of population study could be developed and improved in at least three ways. First, when the

[1] It is thought justifiable to consider that the first parasite to emerge will in all probability be the same species each year.

seasonal appearance and interrelationships of the various species of parasites involved have been worked out as far as possible, the part they play should be considerably clearer. Secondly, in this particular study only the overwintering generation of the midge has been under consideration. Thirdly, twelve years is only a short period during which to observe the effect of weather; a far longer period is to be desired. Data of this nature can be amassed without interrupting other work and in fact it becomes a matter of simple routine. For this reason it is to be hoped that, however indeterminate the present results appear, other workers will be encouraged to accumulate similar data on various insects and rest assured that their work will be of some use. One major difficulty, which apparently everyone will meet, is that with the exception of a few species the parasitic Hymenoptera are inadequately known, while the knowledge of their life histories lags still further behind.

6. Summary

1. This study of the gall midge *Rhabdophaga heterobia* H.Lw. is a continuation of the third study in the series, which covered the years 1928–33, and the data for the years 1934–9 are given. In addition, the results of the whole twelve years, 1928–39, are reviewed.

2. The changes in the total insect population (midge and parasites) have been discussed. Birds are shown to play an important role in reducing the total population during the winter months. The drop in 1930 was probably caused by a drought in the late summer of 1929. The hot summers of 1933 and 1934, acting through the plant growth, caused similar reductions in 1934 and 1935. Since 1936 the population has steadily fallen because the willows have been allowed to go out of cultivation and become exterminated as a result of grazing.

3. A positive correlation has been found to exist between the numbers of midges and parasites, but there is no correlation between the size of the total population (midges and parasites) and the percentage parasitism. The changes from year to year in the numbers of the total population and in those of the parasites are almost identical. It is concluded that relative parasitism as high as 64% exerts no control on the number of midges and also that the parasites do not become more efficient at high population levels than at low ones and so cannot have any balancing effect.

4. The readiness of the midge and its parasites to emerge in response to extra warmth given in March has been demonstrated. Under normal conditions dates of first emergence have varied from 13 April to 16 May in the case of the midge, but the variation is less when the weeks of maximum emergences are considered. The emergence of the parasites usually follows closely that of the midge but in some years the weather appears to act differentially on the midge and its parasites as regards the dates of emergence.

7. Acknowledgements

I am deeply indebted to Mr A. Roebuck for his continued great help in collecting the material and discussing the whole problem. My thanks are also due to Dr C. B. Williams and Dr A. C. Evans for their assistance in the more statistical side of the investigation.

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ON THE SIZE DISTRIBUTION AND BREEDING CYCLES OF FOUR MARINE PLANKTONIC ANIMALS FROM THE ARCTIC

By M. J. DUNBAR

(*With 5 Figures in the Text*)

1. Introduction

Steuer (1933) has indicated the need, in plankton research, for the detailed investigation of coastal waters; Russell (1936) emphasized this amongst other suggestions for the planning of future plankton expeditions. He adds that "especial attention should be paid to a study of the life histories of some of the larger Arctic-boreal species such as *Sagitta elegans* and *Clione limacina*".

The present paper is concerned with the breeding cycles and size distributions of the Chaetognath, *Sagitta elegans arctica* (Verrill), and of three Schizopods, *Thysanoessa inermis* (Kröyer), *T. raschii* (M. Sars), and *Boreomysis nobilis* (G. O. Sars). The material was collected by Mr C. H. Hartley and myself in the summer of 1936, during an expedition to Atâ Sound, situated at the north-east corner of Disko Bay, in West Greenland. These four organisms are found very abundantly in the Arctic, and are ecologically very important. The list of other species found on the expedition, with their distribution and abundance, will be published later. Some of the hydrographic results have already appeared (Hartley & Dunbar, 1938). Full acknowledgement for assistance in equipping and organizing the expedition will be made in the later paper.

2. The hydrography of the area

Atâ Sound lies between N. Lat. 69° 30′ and 70°, its mouth lying 20 miles north of Jakobshavn. It is some 30 miles in length and possesses at its head two tidal glaciers, Kangilerngata Sermia and Eqip Sermia. Since the development and behaviour of planktonic organisms are in close relation to the type of water in which they live, some idea should be given here of the water of the Sound.

Kramp (1918) gives a summary of the hydrographic conditions in Davis Strait. The comparatively warm Atlantic water, which spreads northward in the deeper parts of the Strait is stopped for the most part by the submarine ridge which stretches from Holstensborg to Cape Walsingham in Baffin Island. This water has a temperature of at least 3° C. and a salinity of more than 34·5‰. "North of the submarine ridge, in Disko Bay and Umanak Fjord, the facts are very nearly as in the open Baffin Bay, i.e. setting aside the uppermost layers, directly warmed by the sun, there is an upper stratum, about 200 mm.,

with low, partly negative temperatures and a salinity below 34‰. Below this stratum the temperature is about 1° C., and the salinity more than 34‰."

Since the mass of the zooplankton was found at a depth of from 15 to 30 m., we are concerned here only with the upper 50 or 100 m. Negative temperatures were recorded only twice, not in Atâ Sound itself, but at the mouth of the Jakobshavn Ice-fjord. At all other stations the temperatures from 10 to 100 m. varied only between 0·16 and 2·55° C. The salinities were all below 34‰. Hence no trace of Atlantic water was demonstrable.

The presence of a drainage river from the ice-cap, and of the two glaciers, caused a considerable freshening of the surface water of the inner part of the Sound, the extent of their influence varying with the quantity of ice in the water and the amount of mixing by wave action. The greatest freshening recorded was on 4 July, when the surface salinities ranged from "fresh" to 30·55‰ over a distance of 10 miles from the Eqip glacier. On the other hand, the surface salinity only 3 miles from the glacier, was sometimes as high as 26·8‰. It is in the uppermost 10 m., and probably in the uppermost 5 m. or even less that the intense stratification occurs, both in temperature and salinity. The salinity at 10 m. was always between 31·4 and 33·0‰, and the temperature low, while surface temperatures of 7 and 8° C. were occasionally met with. Large quantities of melting brash ice produced the low temperatures at the surface, and tended to keep the temperature down, so that a combination of low salinity and high temperature is rare.

3. Methods

The nets used were made of close-meshed bolting cloth. This is not the best net for Arctic macroplankton, or for any macroplankton, and I have since had better results with the 1 m. stramin ring-trawl. This is the largest net that can conveniently be used from a small motor-boat. The catches were preserved in 5% formalin in sea water.

After the sorting and identification of the collection, the four species dealt with in this paper, being the largest, most abundant (excluding Copepods), and most amenable to such treatment, were counted, sexed, and measured. The measurements were made under a low-power binocular microscope, using a thin glass slide and a half-millimetre scale. For the smaller specimens, and for the measurement of the ovary of *Sagitta*, a mechanical stage with a vernier scale was used, the material to be measured being brought up to a line on a micrometer eyepiece. In measuring *Sagitta*, the tail fin was not included, since this membrane is subject to damage in handling, nor was the telson included in measuring the Euphausids and Mysids.

In constructing the size-frequency histograms, the specimens were referred to central (pivotal) lengths, in 1 mm. groups (2 mm. groups in the case of the Mysids), and the size distributions were then studied.

4. The organisms investigated, and their size distributions

(*a*) **Sagitta elegans** is a northern Atlantic species, belonging to the mixed oceanic and coastal water. The variety *arctica* (Aurivillius) is an Arctic-boreal neritic form, distinguished by its large size and comparatively short tail segment. Kramp (1918) says of it that it is "the only species among the Chaetognaths of the Arctic which has its principal occurrence in the neighbourhood of the coasts". His specimens from the *Tjalfe* expedition were nearly all found "at a fairly large distance from the surface", in water of about 0·5° C. and between 33·6 and 34·2‰ salinity. It is, however, not surprising that in the shallow water of Atâ Sound it should be found in slightly warmer water than this. Ritter-Záhony (1910) states that in Spitsbergen it is abundant in the shallow water. Huntsman (1919) has found it to be typical of the cold coastal water, to occur over practically the whole of the eastern Canadian continental shelf, and to be confined to water of comparatively low salinity. Except sporadically at the surface, where its presence, except possibly in the very young stages, may be considered as accidental, *Sagitta* was found in Atâ Sound in water of salinity close to 33‰ and at temperatures below 2° C.

Altogether, approximately 900 specimens were obtained. Of these 492 were measured, those caught on three days, 31 July and 5 and 20 August. In water of Arctic temperature, the amount of growth which can take place between these time limits must be negligible, and hence the error incurred in including these specimens in one curve is not significant. The distribution of the size groups is shown in Fig. 1. The histogram is evidently bimodal. An interpretation of the bimodal curve is given in the discussion at the end of the paper.

Of the specimens measured, 135 were stained with Carmalum and mounted for examination of the gonads. The lengths of the ovaries were measured, and the stage of development of the testes recorded. The testes were referred to an index "0–5", being graded from "0", with no trace of "polyblasts" (Bordás, 1912), to "5", with the cavities of the testis packed with polyblasts containing spermatozoa and ripening spermatocytes. There were no spent specimens in the number examined.

Fig. 2 is the growth curve of the ovaries relative to the body length. Each datum point is the mean of the ovary lengths of the specimens, grouped under integer body-length values, and the number of specimens from which the mean was taken is shown beside each point. Plotted on a double logarithmic grid, the points lie fairly closely on a straight line, and hence the ovary shows simple heterogony in its growth in length, obeying the formula, given by Huxley (1932):

$$\log y = \log b + k \log x,$$

where y and x are the magnitudes of organ and body respectively, and b and k are constants. The slope of the curve is unusually steep, the value of k being approximately 3·85. There were, among the specimens stained and examined,

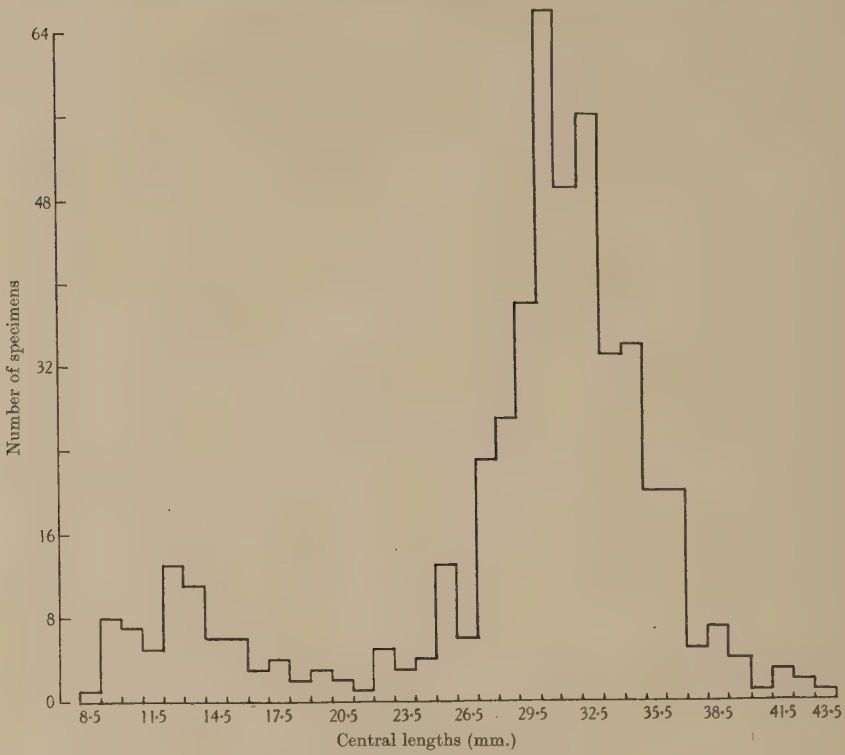

Fig. 1. *Sagitta elegans arctica* 492 specimens.

Table 1. *Size distribution of* Sagitta elegans (*Fig.* 1)

Central length (mm.)	Frequency	Central length (mm.)	Frequency
8·5	1	26·5	6
9·5	8	27·5	23
10·5	7	28·5	27
11·5	5	29·5	38
12·5	13	30·5	66
13·5	11	31·5	49
14·5	6	32·5	56
15·5	6	33·5	33
16·5	3	34·5	34
17·5	4	35·5	20
18·5	2	36·5	20
19·5	3	37·5	5
20·5	2	38·5	7
21·5	1	39·5	4
22·5	5	40·5	1
23·5	3	41·5	3
24·5	4	42·5	2
25·5	13	43·5	1

Total 492

five individuals whose ovaries were large and contained ripening eggs at a very much smaller body length than was normal for the remainder. Such in-

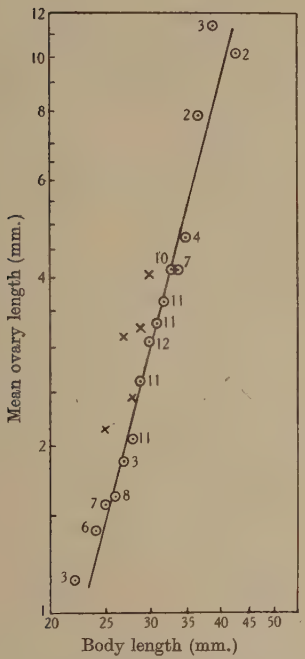

Fig. 2. Growth in length of the ovaries of *Sagitta elegans arctica*. (See text.)

Table 2. *Ovaries of* Sagitta (*Fig.* 2)

Body length mm.	No. of specimens	Mean ovary length (mm.)	Range
11	1	0·0	
12	1	0·0	
13	2	0·0	
14	2	0·44	0·35 – 0·53
15	5	0·37	0·0 – 0·8
16	2	0·8	0·7 – 0·9
17	2	0·68	0·5 – 0·75
18	2	0·55	
19	2	0·89	0·875– 0·9
20	3	0·85	0·5 – 1·1
22	3	1·15	0·55 – 1·6
24	6	1·41	1·2 – 1·7
25	7	1·57	1·3 – 1·8
26	8	1·625	1·0 – 2·5
27	3	1·88	1·6 – 2·2
28	11	2·06	1·6 – 3·4
29	11	2·61	1·9 – 4·25
30	12	3·09	1·8 – 4·3
31	11	3·32	2·0 – 5·7
32	11	3·64	2·1 – 7·9
33	10	4·16	2·25 – 7·9
34	7	4·16	2·45 – 7·0
35	4	4·76	3·15 – 6·45
37	2	7·85	6·1 – 9·6
39	3	11·4	6·3 –17·05
43	2	10·18	9·45 –10·9

The data for body lengths 22–43 are plotted logarithmically in Fig. 2.

dividuals are also mentioned by Kramp (1918). The mean ovary lengths calculated when these "precocious" individuals were included are shown by crosses in Fig. 2. Their inclusion so disturbs the growth curve that it is reasonable to suppose that they belong to a different brood, and that they either represent the last survivors of an earlier breeding period, which is not probable, or have been brought to Atâ Sound with water from elsewhere. From the fact that they are maturing at a much smaller size than the bulk of the catch it might be inferred that they had developed in slightly warmer, and possibly Atlantic, water. The testes of all five of them were in an advanced state of development.

Russell (1932) found that the ovaries, in *Sagitta elegans* from the Plymouth area, do not start to develop until the testis is ripe, or at least filled with ripening spermatocytes, and he was able because of this to classify the animals into three stages of development. From Fig. 2 it will be seen that the ovaries

of *arctica* begin their rapid growth in length when the animal is about 22 mm. long. At this length, the testis is little over half-way to maturity. The testis does not become ripe until the animal has reached a length of some 30–35 mm. (It is not possible to show a definite limit between ripe and unripe testes. Here, following the example of Kramp, the specimens have been called ripe when the cavities of the testis are packed with polyblasts.) Thus it seems that in Arctic waters the ovaries begin to develop sooner, relative to the development of the testis, than they do in temperate waters. A comparison with the development of *S. elegans* in the Plymouth area, as described by Russell, suggests that the difference between the growth rates of the gonads in the temperate and arctic zones is an automatic result of the slowing down of all growth processes in the colder water.

(*b*) **Thysanoessa inermis** is found over the whole of the north Atlantic, and it has also been recorded from the north Pacific (Hansen, 1915). In the Arctic it is the most common Euphausid, the northern counterpart of *Euphausia superba* of the Antarctic. In West Greenland it is known up to the 71st parallel. It has been shown to be a staple food of various whales; the bowhead, north Atlantic right whale (*Eubalaena glacialis*), the common finback (*Balaenoptera physalus*), Rudolphi's rorqual (*Balaenoptera borealis*), the blue whale (*Balaenoptera musculus*), and the humpback (*Megaptera nodosa*) (Allen, 1916). In Atâ Sound and Disko Bay, some 210 specimens were collected. There were also 107 specimens of *Thysanoessa neglecta*. *T. neglecta* was formerly considered to be a separate species, until Hansen (1911) published reasons for regarding *inermis* and *neglecta* as synonymous. The force of his arguments was impressed upon the author during the identification of the catches. It is sometimes impossible to decide whether a given specimen should be referred to one or the other species, in accordance with the older literature. The division of the eye, said to be characteristic of *neglecta*, is occasionally found in otherwise typical *inermis* specimens, and the elongated first pair of thoracic legs is variable. In all other characters the two species appear to be identical. However, since Hansen's work, Lebour (1924) has found that the eggs of the two forms are different in size, that there is a constant difference in the form of the first pleopods of the male, and that the Cyrtopia larvae can be distinguished. It seems, therefore, that the older nomenclature is correct, and that the two species are distinct. The size of the *neglecta* specimens from Greenland was considerably smaller on the average than that of *inermis*, and if they were to be included in the *inermis* size-distribution curve they would all fall in the first, or smaller group. On this evidence, and that of Dr Lebour, *neglecta* has here been considered a separate species, and has not been included in the *inermis* size curve.

To the best of my belief, no work has been done on the breeding cycles of the Arctic Schizopods. The only publications relevant to this are those of the *Discovery* Commission, and the Norwegian Scientific Academy, on the Antarctic

plankton. Thus Ruud (1932) has worked on the life history of *Euphausia superba* in some detail. He found that in the whale stomach contents there were two size groups, significantly distinct, and he adds that this phenomenon is without parallel in our Boreal waters. Fig. 3, made from the catches of 31 July and 5 August, shows the size distribution of *Thysanoessa inermis* from Atâ Sound. There appears to be a broad division into two groups, of which the right-hand one contains also a suggestion of a third mode.

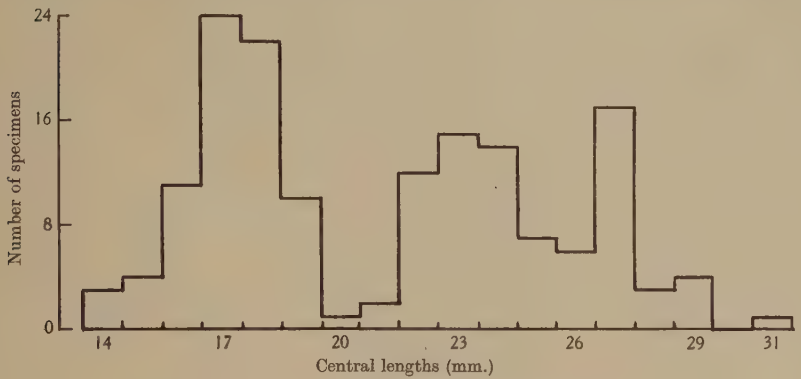

Fig. 3. *Thysanoessa inermis*, 156 specimens.

Table 3. *Size distribution of* Thysanoessa inermis (*Fig.* 3)

Central length mm.	Frequency	Central length mm.	Frequency
14	3	23	15
15	4	24	14
16	11	25	7
17	24	26	6
18	22	27	17
19	10	28	3
20	1	29	4
21	2	30	0
22	12	31	1

Total 156

(*c*) **Thysanoessa raschii** has a distribution roughly coincident with that of *T. inermis*; this species also is known from the north Pacific (Stephensen, 1933). It is less abundant than *inermis*, and is less important as the food of whales and the plankton-eating seals. In Atâ Sound, 160 specimens were caught on 31 July and 5 August. Their size distribution is shown in Fig. 4: it is evidently bimodal.

(*d*) **Boreomysis nobilis** belongs to Arctic waters, and is known from Baffin Bay to Spitsbergen. Most of the specimens of this species, the only Mysid found in any numbers in Atâ Sound, were taken on 30 and 31 July, and 5 August. Fig. 5 shows their size distribution. The curve is heavily loaded on the left by a considerable number of very small immature individuals. To the

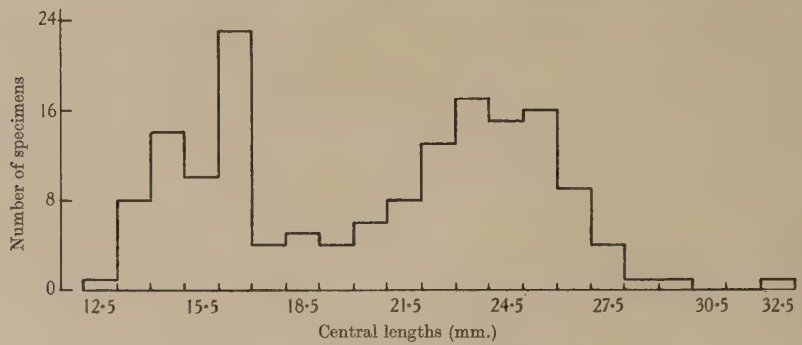

Fig. 4. *Thysanoessa raschii*, 160 specimens.

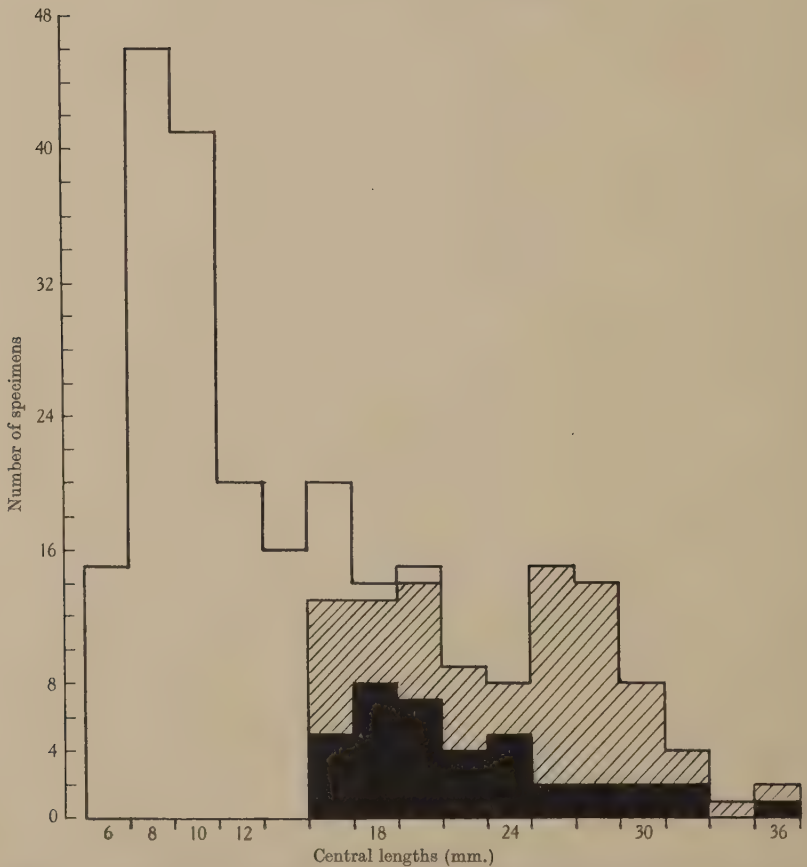

Fig. 5. *Boreomysis nobilis*, 248 specimens. Black = males, Shaded = females, white = immature.

extent to which this is balanced by the mature and maturing individuals on the right, the curve may be taken to represent two separate broods, but the shape of the curve does not justify its division at any one point. It will be seen that the males average slightly smaller than the females; this would in part account for the obscuring of the adult mode. However that may be, the case for *Boreomysis* differs from the rest in that the brood pouches of many of the larger females contained young, all stages from the egg to the nauplius being found in them. Moreover, some of the largest females had spent, or empty, brood pouches. Hence it is quite possible that the left-hand end of the curve represents the offspring of the right-hand end. From these facts it would appear that *Boreomysis nobilis* has a very prolonged spawning period in the summer, extending into the autumn. The length of time required to reach maturity in the Arctic is not known.

Table 4. *Size distribution of* Thysanoessa raschii (*Fig.* 4).

Central length mm.	Frequency	Central length mm.	Frequency
12·5	1	23·5	17
13·5	8	24·5	15
14·5	14	25·5	16
15·5	10	26·5	9
16·5	23	27·5	4
17·5	4	28·5	1
18·5	5	29·5	1
19·5	4	30·5	0
20·5	6	31·5	0
21·5	8	32·5	1
22·5	13		

Total 160

Table 5. *Size distribution of* Boreomysis nobilis (*Fig.* 5).

Central length mm.	Frequency	Central length mm.	Frequency
6	15	22	9
8	46	24	8
10	41	26	15
12	20	28	14
14	16	30	8
16	20	32	4
18	14	34	1
20	15	36	2

Total 248

5. DISCUSSION

From size-distribution studies of this sort, something may be learned of the breeding cycles of the organisms studied. The argument stands on the following assumptions:

(1) That the water in which the animals live is of one type, or at least that any entry of (in this case) non-Arctic water is so slight as not to bring in a population of animals on a different level of the "size-cline" from the Arctic type, such as to disturb the size distributions.

(2) That the populations studied are genetically fairly homogeneous as regards factors regulating size. The existence of two size strains in a population of marine planktonic organisms from a limited volume of monotypic water is very improbable.

In point of fact the existence of both these conditions is upheld by the fact that the smaller individuals, those making up the first mode in the histograms, are all immature.

Under these conditions, bimodal curves of the type published here, in which there are no spent individuals present (and it seems fairly certain that the animals die after spawning), rule out the possibility of a short breeding period in which the whole population takes part, as seems to happen, for instance, several times a year in the Plymouth area in the case of *Sagitta* (Russell, 1932, 1933). Under these conditions normal size distributions are to be expected. There remain two possibilities: (1) that there is a prolonged spawning period, and that the smaller members of the sample represent the offspring of adults which have spawned earlier and have since died, and (2) that there is an overlap of broods. That is to say that the smaller, immature, brood will breed later, probably in the following year, at a time when the offspring of the larger brood are still immature. It has already been shown that in the case of *Boreomysis nobilis* there appears to be a prolonged spawning period of the type just described (1). The behaviour of the Euphausids, however, and of the Chaetognaths, appears to be different, a difference which may be related to the fact that the Mysids brood their young for some time. As far as *Thysanoessa* and *Sagitta* are concerned, the possibility of a prolonged spawning period is rendered unlikely by the facts that the number of fully mature specimens is very small, and that no eggs, or larval stages, were found in the plankton. Hence it is probable that the bimodal size curves represent distinct broods which overlaps in time in the manner described (2).

It remains to show at what intervals the spawning periods take place. To demonstrate this beyond all doubt, a full year's survey is necessary, or at the least a knowledge of the time required by the organisms under discussion to reach full maturity in the Arctic. Ussing (1938), describing the Chaetognaths collected in north-east Greenland by the Danish Three Years' Expedition, says: "the spawning begins at the end of February, when eggs are first observed in the plankton. Even as late as the end of May its eggs may be met with, but after that only the young that have just emerged are seen. There seems to be only one annual generation." Kramp (1918) inclines to the view that the bulk of *Sagitta elegans arctica* in West Greenland breed in the autumn. His collections were made only in the summer. Without the knowledge of the length of time required by *Sagitta* to reach maturity in the Arctic, such collections cannot give conclusive data on the breeding cycles. This applies also to Stott's (1936) conclusions concerning *Sagitta* in Spitsbergen coastal waters. The conclusions of Kramp, and Ussing, however, and of Huntsman & Reid (1921), when taken

together, do suggest that there is only one breeding period in the Arctic. If this were definitely established, then from the present data it would follow that *Sagitta* lives two years in the Arctic waters before the onset of sexual maturity. As to the season of spawning in Atâ Sound, from the examination of the material described, I am inclined to agree with Kramp that the spawning must take place in the late autumn.

The case for the Euphausids, on the present evidence, is much the same as for the Chaetognaths; moreover, there are the results of Rudd's studies, already quoted, by which to estimate new data. In addition to finding bimodal size grouping in the Antarctic *Euphausia superba*, Ruud showed that this species takes two years to reach sexual maturity, and that there is one annual spawning period. Given bimodal size grouping in common, and considering that the hydrographic and organic environment in Arctic waters is similar to that in the Antarctic, it is conceivable that the Arctic Euphausids also live two years from birth to maturity. This conclusion, however, requires confirmation in the field. It is possible that *Thysanoessa* has a shorter lifetime than this, perhaps only one year; it does not grow to the enormous size attained by *Euphausia superba*.

To sum up; there is good reason to suppose that while *Boreomysis nobilis* has a prolonged spawning period in the summer and autumn in Arctic West Greenland, *Sagitta elegans arctica*, *Thysanoessa inermis*, and *T. raschii*, breed at intervals which alternate, that is to say that there are two broods present at any given time, and that one brood will be only half-way to sexual maturity when the other one spawns. It is very improbable that there are more than two spawning periods in the year in the Arctic; there may be only one. There are indications that *Sagitta* has only one spawning period, and therefore that the individual takes two years to reach maturity. For the confirmation of this, and for the further investigation of the Euphausid cycles, it will be necessary to carry out at least one year's survey of the plankton.

6. Summary

1. Size-distribution histograms are given of four Arctic marine planktonic animals from West Greenland: *Sagitta elegans arctica*, *Thysanoessa inermis*, *T. raschii*, and *Boreomysis nobilis*.

2. The growth of the gonads of *Sagitta elegans arctica* is investigated. The growth of the ovaries, plotted against the body length, approaches closely to a logarithmic straight line, within certain size limits.

3. *Boreomysis nobilis* probably has a prolonged breeding period during the summer and autumn.

4. The bimodal size curves of *Thysanoessa inermis* and *raschii* and *Sagitta elegans arctica*, apparently represent distinct broods whose breeding cycles overlap each other.

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CANADIAN ARCTIC WILD LIFE ENQUIRY, 1938–39[1]

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(*With 4 Figures in the Text*)

1. Introduction

In this report information about the fourth of the biological years 1935–39 is presented. The data are opinions on lemmings (*Lemmus* and *Dicrostonyx*), the arctic fox (*Alopex lagopus*), snowy owl (*Nyctea nyctea*) and sledge dog, from 25 annual zoological questionnaires of the Northwest Territories Administration and from over 70 of those of the Hudson's Bay Company. The Bureau of Animal Population is once again indebted to those who have made these reports available for study.

2. Methods

Since no biological research stations are as yet established in the Canadian Arctic, the only way of getting information is by analysing the observations of men living there. Few of these will have had a scientific training, so that satisfactory help can only be expected if (1) the animals are well known to them; (2) the observations required are simple. Arctic fox and snowy owl are familiar to all in the Arctic, and lemmings are in many areas the only small rodents. Where the ranges of lemmings and voles overlap it is certain that the difference between them is not always known, and for this reason information on "mice" is also listed.

The first observation asked for is a comparison of abundance in one year (ending 31 May) with that in the year before. This is fairly simple in the case of the arctic fox, an animal of vital concern to everyone in the north. However, the sudden changes in numbers—whether through migration or death –that may occur within 12 months, sometimes make a single statement for the whole period impossible. In certain years changes in density may be so slight that subjective estimates inevitably vary; but differences on a sufficiently large scale lend themselves admirably to a study by questionnaire methods. Similarly, changes in small rodent populations may at times be hard to observe, often because the density remains low or high in two consecutive years; but again, big changes cannot fail to be noticed. In places, more especially in the Western Arctic, observers have found changes in the snowy owl population very hard to estimate during 1935–39; and this is almost certainly because few of these birds were to be seen at any time.

The second observation required is whether the animals were unusually abundant or unusually scarce (or neither). The replies to this are much less

[1] Promoted by the Northwest Territories Administration of the Canadian Government, Ottawa. The work at Oxford has mainly been carried out with the aid of a grant from the Carnegie Institution of Washington.

useful than the comparative estimates, and the differences between "not specially abundant" (×), "abundant" and "unusually abundant" do not lend themselves to profitable analysis. However, the distinction between extremes of scarcity and abundance is valuable; particularly when no change is reported. In Table 1 of the present report "abundant" and "very abundant", "scarce" and "very scarce" are both indicated a. or s.; the inclusion hitherto of separate categories v.a. and v.s. has not proved justifiable.

A certain proportion of error is unfortunately shown in the replies, but no selection of evidence is considered permissible. Questions about disease and migration have not yet yielded any considerable body of information (except about sledge dogs).

The opinions on comparative abundance are summarized by counting the replies in groups (Table 2) and by showing the areas they refer to on a map for each species (Figs. 1–4). The geographical grouping is somewhat arbitrary; but since the data are presented in detail, analysis and regrouping may be carried out as the evidence demands.

Table 1. *Summary of original data on arctic fox, lemmings, "mice", snowy owl and sledge dog (part) for* 1938–39

The following abbreviations are used: I. = increase, D. = decrease, N. = no change, s. = scarce, × = not noticeably scarce or abundant, a. = abundant.

Sledge dogs: 0 = disease reported absent. 0* = slight disease or starvation reported, + = more serious disease; details in Table 3.

Square brackets indicate observations that have been partly or entirely omitted from maps or summaries (Table 2): (1) Parts or all of some areas are not mapped if they are certainly outside the animal's range; (2) In groups 2 and 3 reports from inland posts are not mapped fully or included in Table 2; (3) Reports on "mice" and events at special times of the year are not counted in Table 2.

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received from the Hudson's Bay Company.

	Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
Group 1. Northern Labrador coast					
Frenchman's Island, outside islands and 20 miles inland	D. s.	[N. ×]	N. ×	D. s.	0
Cartwright and 80 miles inland	D. s.	—	I. a.	D. s.	0
Rigolet, south 50, north 75, west 35 miles	D. s.	I. s.	I. a.	I. a.	0*
Northwest River [and inland 500 miles]	I. ×	—	I. a.	—	0*
Makkovik, 30 miles north and south [and inland, north and north-west, 100 miles from post]	I. ×	N. ×	I. a.	N. ×	0*
Hopedale and 30 miles radius	D. s.	—	I. a.	D. s.	—
Davis Inlet and 30 miles radius	I. ×	I. ×	I. a.	I. ×	0
Voisey's Bay, north-east 108, north 85, north-west and south-west 40 miles	I. a.	I. a.	I. a.	I. s.	0
End of January	[D. s.]	—	—	—	—
Nain, 35 miles north and south; north and north-west 75 miles	I. a.	I. a.	I. a.	I. ×	0
20 *December*	[D.]	—	—	—	—
Nutak and 25–35 miles radius	N. ×	I. ×	I. a.	N. ×	0
Fall	a.	—	—	—	—
Hebron and from Sedlik to Napartok Bay; inland up to 90 miles	I. ×	D. ×	D. ×	D. s.	—

Table I (*continued*)

	Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
Group 2. Coast of Northern Quebec, south to Richmond Gulf [and inland]					
Georges River and 50 [to 150] miles radius	D. s.	D. s.	D. s.	D. s.	—
Inland *in summer*	a.	—	—	a.	—
Whale River to Georges River and inland to just within the tree line	D. ×	I. a.	I. a.	I. a.	0
Summer and early fall	a.	—	—	—	—
Fort Chimo and vicinity	D. s.	I. a.	I.	I.	—
Until middle of November	a.	—	—	—	—
[Fort McKenzie and 120 miles radius]	[I. s.]	[D. s.]	I. s.	—	—
Leaf River, Leaf Bay and coastal area 40 miles east	D.	D.	D.	—	—
Spring	—	a.	—	a.	—
Payne Bay	D. s.	D. s.	D. s.	D. s.	0*
Diana Bay: from Cape Hopes Advance to Payne Bay, west to Burgoyne Bay	D. s.	D. s.	D. s.	D. s.	—
Stupart Bay to Cape Weggs and Burgoyne Bay; inland 100 miles	—	—	D. s.	D. s.	—
Sugluk West and 80 miles radius	D. s.	D. s.	D. s.	D. s.	0
Wolstenholme; east to within 20 miles of Sugluk, south 72 miles to Kovik River	D. s.	D. ×	D. ×	D. s.	0
Mansel Island	D. s.	—	—	I. a.	0
End of May	a.	—	—	—	—
Cape Smith, inland 50, south 20 and north 70 miles	D. s.	D. s.	—	D. s.	—
Late Spring	[I.]	[I.]	—	[I.]	—
Povungnetuk to Cape Anderson and Kogaluk Bay	D. s.	D. ×	D. s.	D. ×	0
Port Harrison, north to Koklak River, south to Nastapoka River	D. s.	D. s.	D. s.	D. ×	0
Group 3. South parts of Hudson Bay, James Bay [and inland]					
Great Whale River north to Little Whale Point, south to Cape Jones, [inland to height of land]	D. s.	[D. ×]	D. ×	I. a.	+
June to September	a.	—	—	—	—
Fort George; north 100, south 50, inland [100] miles	D. s.	[D. ×]	D. s.	—	0
[Kanaapuscow, north 100, south 50, east 175, west 150 miles]	[D. s.]	—	D. s.	—	—
Eastmain, north 60, south 20 [inland 200] miles	D. s.	—	N. ×	N. s.	+
[Neoskweskau and 50 miles radius]	[D. s.]	—	N. ×	—	0
Albany	—	—	D. s.	—	—
Attawapiskat, south to the Lawashi River, [150] miles inland, north to Ekwan River. Also Agamiski Island	N. ×	—	D. s.	N. ×	+
Lake River, south 25 miles, inland to Opinega Lake and north to Trout River	D. s.	—	D. s.	N. ×	—
Until November	—	—	a.	—	—
Weenusk, along the coast north 80, south 60, and inland 100 miles	N. s.	—	N. a.	N. s.	—
Severn, along the coast north-east to Kaskatamagan, south-east to Weenusk and inland [half way to Trout Lake]	I. ×	—	D. s.	N. s.	0*
Late Winter	[D. s.]	—	—	—	—
York Factory and 90 miles radius	D. s.	—	D. s.	N. ×	0
Group 4. West coast of Hudson Bay, north from Nelson River and inland					
Caribou and 50 miles radius	D. s.	D. s.	N. ×	N.	0
Nonala north to north branch of Big River, south to Hubbart Point, inland 50 miles	D. s.	D. ×	D. ×	D. ×	0
On the ice *in April*	[I.]	—	—	—	—

Table I (*continued*)

		Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
5.	Lat. 59°–61°. Hudson Bay coast and 90 miles inland	s.	D.	—	D. ×	0
13.	Lat. 60°–61° and from Nueltin Lake to within 50 miles of Hudson Bay coast	D. s.	D. s.	—	s.	—
	Churchill (north to Eskimo Point, west to Nueltin Lake)	—	—	—	—	0
	Nueltin Lake to Ennadai Lake	I. a.	D. s.	D. s.	N.	0
	Eskimo Point, north and south 50, west 150 miles	D. s.	D. s.	D. s.	D. ×	0
	North-west of this area	a.	—	—	—	—
10.	Eskimo Point, west 200 miles and from Lat. 60°–62°	s.	I. ×	—	N. ×	0*
	Padley and 8 miles radius	D. s.	D. s.	D. s.	s.	0
	Until 10 *November*	a.	—	—	—	—
	Tavane, north and south 75, west 100 miles	D. s.	D. ×	—	I. a.	+
	Chesterfield Inlet to Cape Fullerton; south to Rankin Inlet and 100 miles inland	D. ×	N. ×	—	I. ×	+
24.	Chesterfield Inlet to Rankin Inlet	D. ×	I ×	—	I. ×	+
	Baker Lake and 120 miles radius	N. ×	N. ×	—	D. s.	0
20.	Baker Lake to Beverley Lake and between Lat. 64°–65°	N. ×	N. ×	—	s.	0
	Group 5. Southampton Island, Repulse Bay and Melville Peninsula					
	Repulse Bay and 15 miles radius	D. ×	I. ×	—	I. ×	+
	Southampton Island (whole island)	D. ×	I. ×	I. ×	I. a.	—
	Group 6. Southern Baffin Island					
	Lake Harbour east to Gabriel Strait, west to Markham Bay	D. ×	D. ×	—	D. ×	0*
17.	Lake Harbour and south coast from Frobisher Bay to Foxe Basin	D.	D. s.	—	D. s.	0
	Cape Dorset and Foxe Peninsula	D.	I. ×	—	s.	0
	Late Spring	I.	—	—	—	—
	Frobisher Bay (post) and from Cape Haven round the bay to Newell Sound	D. s.	D. s.	—	D.	0*
	Head of Frobisher Bay, *late May*	a.	—	—	—	—
	Pangnirtung and Cumberland Sound	D. ×	D. ×	—	D. ×	0
21.	Pangnirtung Fjord and Cumberland Sound	D. s.	N. s.	—	s.	0*
	Group 7. Northern Baffin Island and north					
	Clyde River to Coutts Inlet and Home Bay	D. ×	D. s.	—	D. s.	0*
22.	Pond Inlet, south to Home Bay, south-west to Igloolik, north to Lancaster sound; Bylot Island	D. ×	D. s.	—	D. s.	0
	Pond Inlet, Eclipse Sound and Navy Board Inlet	D. ×	D. s.	—	D. s.	+
	Arctic Bay and all of Admiralty Inlet	D. ×	s.	—	D. ×	+
23.	Craig Harbour, Ellesmere Island	I.	I. s.	—	—	0
	Group 8. Boothia Peninsula and islands west and north					
	Fort Ross, north Boothia Peninsula, south Somerset Island and Prince of Wales Island	I.	D.	—	—	+
	King William Island and Boothia Isthmus (Group 8); Adelaide Peninsula (Group 9)	D. ×	D. s.	—	D. s.	+
	Cambridge Bay and 50 miles radius	I. a.	N. ×	—	—	+
18.	Richardson Island to Walker Bay (see also Group 11)	†I. a.	—	—	—	+

† Counts as a half vote in Table 2.

Table I (*continued*)

		Arctic fox	Lemming	["Mice"]	Snowy owl	Sledge dog
	Read Island to Lady Franklin Point and to north shore of Prince Albert Sound	I. a.	I. a.	—	I. ×	+
	Spring	—	[D. s.]	—	—	—
	Fort Collinson and 60 miles radius	I. a.	I. a.	—	I. a.	+
	Group 9. Pelly Bay, west to east of Coppermine River and inland to Back River					
	Perry River and 50 miles east and west	D. ×	D. s.	—	D. s.	+
19.	Wilmot Island, Kent Peninsula and on the mainland from Cape Barrow to Gray Bay	D. s.	—	—	—	+
	Byron Bay, Victoria Island (Group 8)	D. ×	—	—	—	—
	Bathurst Inlet: west coast from Wollaston Point south to Western River and inland 100 miles; east coast from Gordon Bay to Western River and inland 50 miles. Also Lakes Finnie and Beechey	I. ×	N. ×	I. a.	N. s.	+
	Group 10. Dubawnt Lake, west to Fort Rae and Fort Resolution					
	Fond du Lac: north towards Wholdaia Lake	I. a.	N. ×	N. ×	—	0*
	Stony Rapids: north 300 miles	I. a.	—	I. a.	D. s.	—
	After February	s.	—	—	—	—
	Snowdrift north to Artillery Lake [south to Fort Smith]	I. a.	—	—	—	0*
6.	Ptarmigan Lake, Clinton Colden Lake	I. ×	D. s.	—	N. s.	—
	Early December	[D. s.]	—	—	—	—
	Fort Reliance	—	—	—	—	0
3.	North of west end of Aylmer Lake	I. ×	D. s.	—	D. s.	—
	Fort Reliance	—	—	—	—	0
1.	MacKay Lake	—	N.	—	s.	0
12.	Headwaters of Coppermine River, Lac de Gras east to height of land, north to Fry Lake	N. s.	I. a.	—	I. s.	0
9.	Lake Providence	I.	I.	—	s.	—
	Fort Rae and district	—	—	—	—	+
	Yellowknife to Trout Rock, Goulet Bay and Gordon Lake	I. a.	—	I. ×	N. ×	0
	Fort Rae, south-east 80, north and north-east 150 miles	I. ×	N. a.	N. a.	s.	+
	Group 11. Coppermine River to Alaska					
	Coppermine	N. ×	D. s.	I. a.	N. s.	+
	Fort Dease and east and north-east shore of Great Bear Lake	N. s.	N. ×	I. a.	N. ×	0
15.	East side Great Bear Lake from 30 miles north of [Port Radium] to south end McVicar Arm	I. ×	—	I.	D.	0
18.	Cape Krusenstern to Bathurst Inlet (see also Group 8)	†D. s.	D. s.	—	D. s.	—
	Both the above and also further west to Stapylton Bay (mainland) and on Banks Island [? locality]	—	—	—	—	+
	Baillie Island to Horton and Anderson Rivers	I. ×	D. s.	—	—	+
	Tuktuk to Mackenzie Delta and Kugalook	I. ×	D. s.	I. a.	I. ×	0*
14.	Richards Island to Anderson River	D. s.	D. s.	—	D.	+
8.	Lower Mackenzie Delta	N. ×	—	D.	N. s.	0
	Aklavik to Point Separation, to Shingle Point and Kittigazuit	N. ×	N. ×	I. ×	D. ×	+

† Counts as a half-vote in Table 2.

Table 2. *State of arctic fox, lemming and snowy owl populations in* 1938-39. *Number of observers reporting relative abundance compared with* 1937-38

	Eastern Arctic									Western Arctic					
Group no. ...	1	2	3	4	5	6	7	Total	%	8	9	10	11	Total	%
Arctic fox:															
Increase	6	—	1	1	—	—	1	9	**16**	4½	1	8	3	16½	**64**
Decrease	4	12	5	8	2	6	4	41	**75**	1	2	—	1½	4½	**17**
No change	1	—	2	2	—	—	—	5	**9**	—	—	1	4	5	**19**
	11	12	8	11	2	6	5	55	**100**	5½	3	9	8½	26	**100**
Lemming:															
Increase	5	2	—	2	2	1	1	13	**30**	2	—	2	—	4	**19**
Decrease	1	9	—	8	—	4	3	25	**58**	2	1	2	5	10	**48**
No change	1	—	—	3	—	1	—	5	**12**	1	1	3	2	7	**33**
	7	11	—	13	2	6	4	43	**100**	5	2	7	7	21	**100**
Snowy owl:															
Increase	4	3	1	3	2	—	—	13	**27**	2	—	1	1	4	**22**
Decrease	4	9	—	4	—	4	4	25	**51**	1	1	2	4	8	**45**
No change	2	—	6	3	—	—	—	11	**22**	—	1	2	3	6	**33**
	10	12	7	10	2	4	4	49	**100**	3	2	5	8	18	**100**

3. Results

Lemmings. In 1937–38 increase among lemmings was reported fairly generally in the Eastern Arctic except from the west coast of Hudson Bay. During 1938–39 increase was still reported from parts of Northern Labrador and west through Whale River to Fort Chimo. For example it was stated from Whale River: "The natives blame the abundance of mice and lemmings for the difficulty of trapping white fox, which do not seem to be hungry." Elsewhere the most usual report was decrease.

Observers have indicated that on Baffin Island and (with less uniformity) along the northern coast of Quebec, lemming populations followed more or less the same trends during 1935–39. Omitting Whale River and Fort Chimo, reports of increase from these parts have been as follows (one report of no change is included for both years 1937–39; i.e. after increase the year before.)

	1935–36	1936–37	1937–38	1938–39
Part of groups	2 6 7	2 6 7	2 6 7	2 6 7
Proportion of increase reported	2/8 2/7 0/6	8/11 6/6 4/4	10/11 6/6 2/3	0/9 2/6 0/3
%	19	86	90	11

Clearly a peak was reached in 1937–38 and passed the following year.

On Southampton Island and south down the coast from Repulse Bay to Nonala (omitting reports from inland) events were certainly different. The next list shows the number and kind of reports in the vicinity of the main settlements.

General vicinity	1935–36	1936–37	1937–38	1938–39
Southampton Island	I. ×	D. s.	I. ×	I. ×
Repulse Bay	I. × I. ×	D. s.	I. a.	I. ×
Chesterfield Inlet	I. × I. D. s.	D. s.	D. s.	I. × N. ×
Tavane	I. I. ×	I. a.	N. ×	D. ×
Eskimo Point	I. a. I. a.	I. a.	N. D. ×	I. × D. s.
Nonala	D. s. N. I. s.	I. I. ×	D. ×	D. D. ×

Increase was generally apparent in 1935–36, but in the next year was confined to the south parts of the region, while on Southampton Island, at Repulse Bay and Chesterfield Inlet lemmings decreased. During 1937–39 lemmings on Southampton Island and at Repulse Bay were recovering; at Tavane, Eskimo Point and Nonala they seem on the whole to have been decreasing. At Chesterfield Inlet some recovery was apparently noticeable in 1938–39, and the increase reported in snowy owls is further circumstantial evidence.

These statements cannot be supported by a convincing body of statistics, or even be given in precise terms; but the difference between these reports and those from Quebec and Baffin Island does, in all probability, reflect a real difference of phase in the lemming fluctuations.

In the Western Arctic the lemming populations seem to have behaved in a more local manner than in the east. At Fort Collinson and Read Island on the west coast of Victoria Island a peak in numbers may have been reached during 1938–39, after two years of recovery from decrease in 1936–37. From Read Island it was stated: "In the fall 1938 lemming were everywhere. This spring there is not one to be seen. Where they went is a mystery. No dead ones have been found." Around the headwaters of the Coppermine River increase and no change (abundant) are reported. Decrease occurred in the vicinity of Fort Ross and King William Island and all along the coastal mainland.

Arctic fox. In the Eastern Arctic the most significant feature of the present reports is the contrast with 1937–38, a year in which foxes were increasing almost everywhere. In 1938–39 the only region where a majority of observers reported increase was along the Northern Labrador coast. As at Severn, Ont., the increase at two of the posts was not maintained throughout the year. Almost everywhere else a decline in the fox population is reported for the year as a whole.

On the other hand, two large regions in the Western Arctic seem to have experienced an increase in foxes: (1) Fort Ross vicinity and Victoria Island; (2) Bathurst Inlet and the barren lands to the south. Between these two regions, including the islands and coastal mainland from Boothia Isthmus to beyond Coppermine reports were of decrease (four) or no change (one). West from Baillie Island no obvious general trend in fox numbers is evident.

Snowy owl. That significant changes in the numbers of this species can be established by the questionnaire method is best shown by the reports of increase for Baffin Island (one report of no change is included for 1937–38):

	1935–36	1936–37	1937–38	1938–39
Proportion of increase reported	5/15	9/9	5/10	0/8
%	33	100	50	0

As suggested in the preceding report, the evidence for 1937–38 was of the passing of a peak in snowy owls, possibly because the food supply was starting to fail.

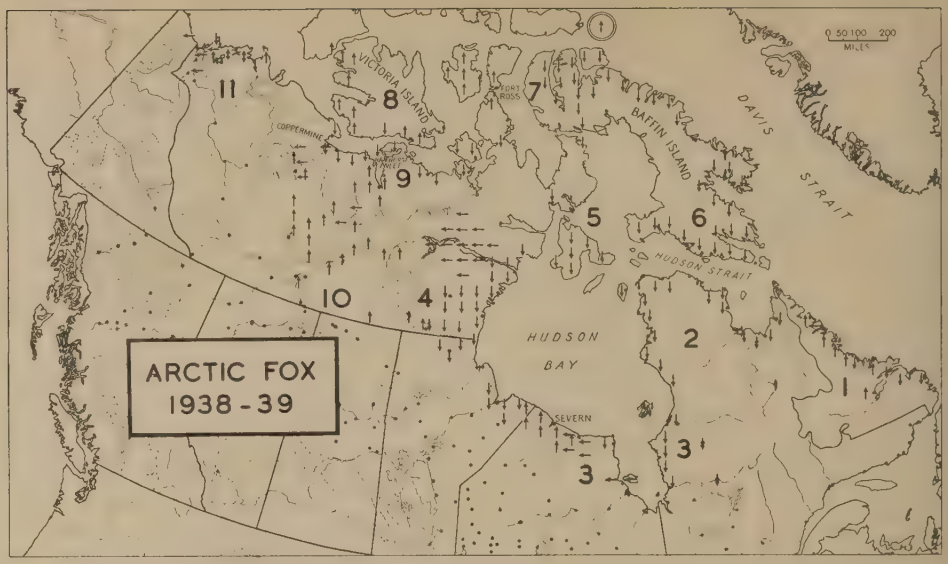

Fig. 1. State of the arctic fox population in 1938–39 compared with 1937–38. Arrows indicate the areas covered by observers reporting INCREASE (↑), DECREASE (↓), and NO CHANGE, NOT ABUNDANT (←). Small black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. Inset: Craig Harbour, Ellesmere Island.

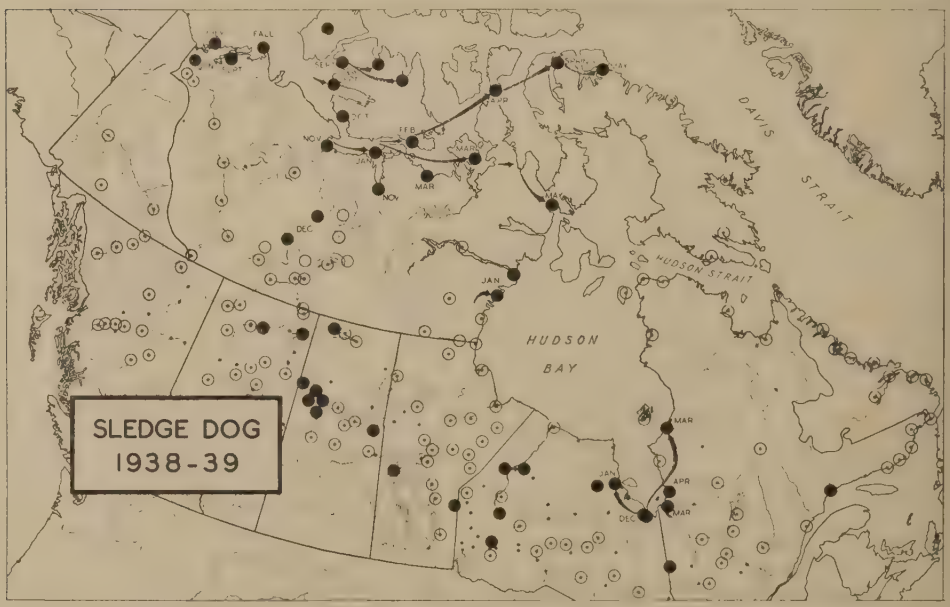

Fig. 2. Prevalence of disease among sledge dogs in 1938–39. Reports of serious disease are indicated ●; disease entirely absent: ○; other reports: broken circle. Arrows show the source from which disease was believed to have been contracted. Months shown are those in which the first outbreaks occurred at each place. Small black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones.

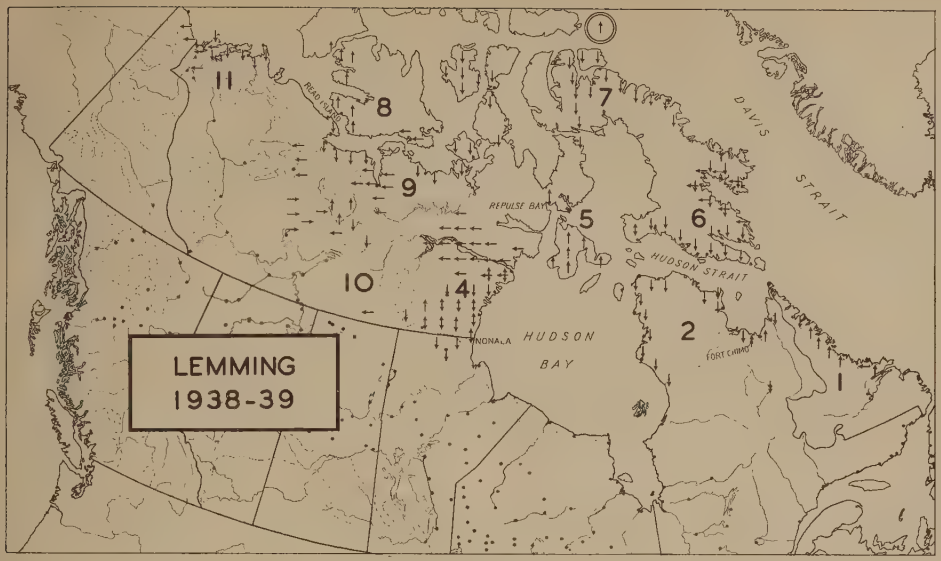

Fig. 3.

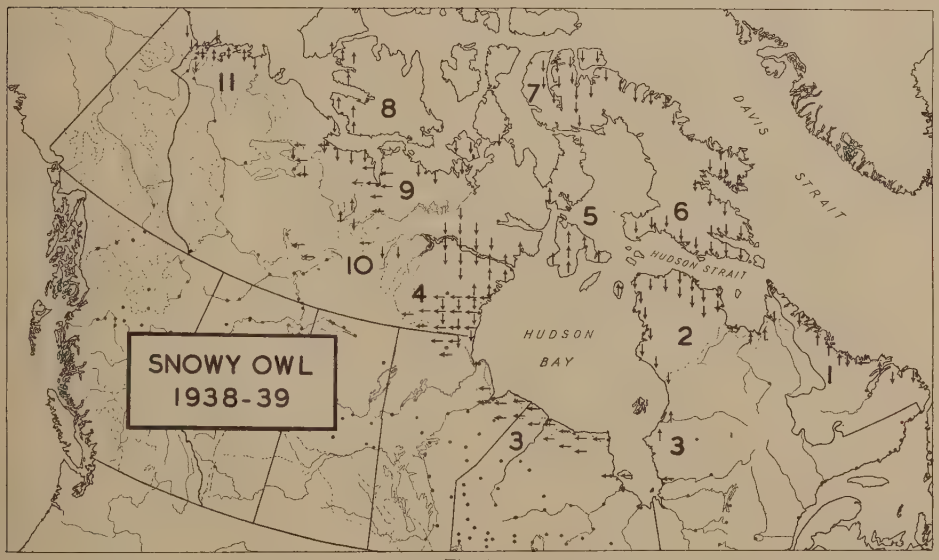

Fig. 4.

Figs. 3, 4. State of the lemming and snowy owl populations in 1938–39 compared with 1937–38. Arrows indicate areas covered by observers reporting INCREASE (↑), DECREASE (↓), NO CHANGE, NOT ABUNDANT (←) and NO CHANGE, ABUNDANT (→). Small black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. Inset: Craig Harbour, Ellesmere Island.

Along the north shore of Quebec there was not such a general increase in 1936–37. The proportion of reports of increase was the same in both the years 1936–38 (7 out of 12), though the distribution was different. At only two out of 13 localities was no increase reported in at least one of these years; while for 1938–39 as a whole it was only noted at three posts.

In Northern Labrador there were 10 out of 10 reports of increase in 1937–38, four in 1938–39 and two of no change. The fairly general abundance of small rodents is no doubt why there has been less decrease reported here than in groups 2, 6 and 7.

In the west no general peak in numbers has been apparent in the four years, but there have been correlations with increase in lemmings at individual posts. This correlation of snowy owl increase with that in lemmings is also shown in the following abstract from Table 1 of the present report:

Group	Distribution of increase reports for snowy owls	Reports on lemmings	Reports on mice
1	Rigolet	I. s.	I. a.
	Davis Inlet	I. ×	I. a.
	Voisey's Bay	I. a.	I. a.
	Nain	I. a.	I. a.
2	Whale River	I. a.	I. a.
	Fort Chimo	I. a.	I.
	Mansel Island	—	
	Cape Smith (*late spring*)	I.	
3	Great Whale River	D. ×	D. ×
4	Tavane	D. ×	
	Chesterfield Inlet	N. × I. ×	
5	Repulse Bay	I. ×	
	Southampton Island	I. ×	
8	Read Island	I. a.	
	Fort Collinson	I. a.	
10	Headwaters of the Coppermine River	I. a.	
11	Tuktuk	D. s.	I. a.

The list shows 17 localities at which snowy owls were reported as increasing, and at 13 of them so were lemmings. There was a correlation with "mice" at Tuktuk, no correlation at all at Great Whale River or Tavane and one incomplete report.

Sledge dogs. During 1937–38 sledge dog disease was mainly confined to settlements along the Mackenzie River. Throughout 1938–39, however, severe outbreaks of disease wreaked havoc among teams from the Mackenzie Delta to the Eastern Arctic. Information from the reports is fully documented in Table 3 and is mapped in Fig. 2. The general belief is that the disease was "distemper" and in many cases that it was spread from west to east by visiting teams. Descriptions, and dates of the first outbreaks support these views. There is no evidence of "crazy disease" except at Repulse Bay or of a relation between this pandemic and disease in wild life.

There was also disease on the west coast of Hudson Bay and in the James Bay region. Here and there deaths occurred through starvation because of the hard winter and the consequent difficulties in hunting. At the more southern posts of the Hudson's Bay Company epidemics were not nearly so widespread as in the Arctic.

Table 3. *Information about sledge dogs*, 1938–39

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received from the Hudson's Bay Company. Reports of serious disease are marked + in this table and shown by a solid circle on the map. Outbreaks apparently less serious, deaths through starvation, etc. are shown by a broken circle on the map. Absence of trouble is shown by a full circle; but names of these posts, other than those given in Table 1, are not listed. Not more than one symbol is given for each report except where indicated (2+ etc.). Fuller descriptions of some of the areas are in Table 1.

Quebec and Labrador.

\+ *Seven Islands.* "Disease in May: blocked nose, paralysis of hindquarters. 15% affected and all died."

Rigolet. "No disease; but some died from starvation due to the very inclement weather of February when the owners found it impossible to hunt seals. Seals were very scarce all through the winter, consequently several dogs died from lack of food."

Northwest River. "There are very few sledge dogs in this vicinity, but a few were sick during January. The attack was of a mild type, the dogs frothing at the mouth with no inclination to move around or work. Very few, if any, died."

Makkovik. "There was no disease among sledge dogs in this vicinity. A few dogs died, presumably through starvation, due to scarcity of feed."

Payne Bay. "Epidemic among sledge dogs in January, February and May: apparently stomach trouble, but fortunately only five deaths occurred."

\+ *La Sarre.* "Some dogs sick this winter and about 10% died. Outbreak noticed at end of January and early in February. Symptoms: coughing, then pus running from nose and eyes."

Ontario.

\+ *Lac Seul.* "Distemper broke out amongst sledge dogs and nearly all in this area died."

\+ *Cat Lake.* "Distemper spread among the Indians' dogs last November killing nearly all. Symptoms: running at nose and eyes, foaming at mouth, starving."

\+ *Bearskin Lake.* "Outbreak about 1 January 1939: mattery eyes and nose, unable to eat for days."

\+ *Trout Lake.* "Outbreak in March, running eyes and nose followed by fits before death. About 50% mortality. Apparently brought through from Bearskin Lake."

Manitoba.

\+ *Little Grand Rapids.* "In July and August many of the dogs around this area died with some kind of disease in the stomach causing swelling. Dogs were constipated. Death, in a week or two at most, removed 10–20% of the dogs."

Poplar River. "Quite a few dogs died at the fish camps and the chief disease seems to be worms."

\+ *Cedar Lake.* "Distemper in March and April. This is the first year it has really been bad."

Oxford House. "No disease: but many deaths among Indian dogs due to starvation."

Saskatchewan.

\+ *Pelican Narrows.* "Very bad last season: started in late September when two out of three dogs died. Trouble started with worms, developed into severe dysentery and general wasting away. Average length of sickness before death: 4–6 weeks."

\+ *Isle à la Crosse.* "Slight outbreak of distemper in April with 25% mortality

Table 3 (*continued*)

+ *Pine River.* "Distemper took a large proportion of sledge dogs. Outbreak occurred in November and December: mortality about 60%. More old dogs afflicted than young ones."

+ *Buffalo River.* "Distemper occurred during March. About 50% of the dogs were affected and about half of these died."

+ *Clear Lake.* "Some type of distemper in late March, April and early May. Mostly young dogs and pups affected: about 30% attacked and approximately 25% of these died. Peculiar aftermath: semi-blindness, no control of limbs, partial paralysis."

+ *Portage la Loche.* "In December many dogs died seemingly of a kind of anaemia, some with big belly and distemper symptoms."

Fond du Lac. "Distemper broke out in April but not serious: a few dogs died. They appeared to have cramps or paralysis of the hind quarters and bled at the nose."

+ *Goldfields.* "Distemper in March and April: pus running from nose, and eyes affected. About 25% died."

Alberta.

Trout Lake. "Epidemic in December and January. Sort of distemper, dogs could not eat. About 10 died."

+ *Fort Chipewyan.* "Disease broke out in March causing about 50 deaths: roughly 5% of the dog population and 25% of those affected. Symptoms: discharge from eyes and nose and swelling of head."

+ *Little Red River.* "Outbreak in March. Disease lasted about two days before the dogs died. About 30 dogs died over a period of 6–8 weeks."

Upper Hay River. "Sickness was noticed during March. Dogs vomited a lot and would not eat. Although the attack was general, it only lasted for about three weeks and was of a very mild nature as only about 4% of the dogs died.

Yukon Territory.

Fort Francis. "Perhaps five or six dogs died early in the winter: possibly they were starved; but the natives said they died of disease."

Northwest Territories.

1. Mackenzie River Valley

Wrigley. "Disease in January. Symptoms: stopped in the middle of play, vomited yellow matter, foamed at mouth, lived two days without eating and died third day. Disease, which we take to be distemper, did not spread universally and cases of death were in isolated ones and twos."

Fort Norman. "About 10 of the Indians' dogs on the west side of the Mackenzie River died; but this is thought to have been due to malnutrition due to lack of game and fish."

Arctic Red River. "A few dogs died during January and February. We believe they died from the hardships endured during that cold period through lack of sufficient food. No disease broke out in the spring."

2. *Arctic Red River.* "October–December slight distemper."

+ *Aklavik.* "Serious outbreak June to August—majority of natives suffered heavy losses among their dogs. Symptoms: running of eyes and nostrils, intense thirst, lack of appetite, no bowel movement, skin dry and coat lacks usual lustre, finally paralysis of hind quarters. After death dogs found in emaciated condition."

2. Great Slave Lake Region

+ *Fort Rae.* "Disease reported among sledge dogs from December to February. Symptoms were: loss of appetite, diarrhoea, vomiting. Disease in almost all cases proved fatal after three days to a week of sickness. Total number of dogs contracting disease was reported as being approximately one out of every five."

+ **9.** *Fort Rae.* December to February: vomiting, dysentery, weak and unable to eat or work for a week. First reports reached Rae in December from Indians in the vicinity of the barrens

Table 3 (*continued*)

around Snare Lake that the sickness was affecting all the dogs. Later similar sickness was reported around Marten Lake [not located]. In January after the annual influx of Indians from northern districts the settlement dogs were affected (R.C.M.P. dogs at Rae were unaffected due to being isolated.) In February reports reached Rae that dogs along the shores of Slave Lake were also affected and some deaths were reported." (2+)

Snowdrift. "A few cases of distemper among pups in spring."

3. Northern coastline

\+ **14.** *Richards Island.* July and August and at east side of Eskimo Lakes a couple of months later. Pus from eyes, sneezing, get weak back and cannot use hind legs: a few get crazy. Old dogs seemed to get sick and die more than pups. Some dogs got well but were not nearly as good as before." (2+)

Tuktuk. "Outbreak in July 1939. Dogs very listless and would not eat. Sickness lasted three days before they died." Not mapped:? July 1938.

\+ *Baillie Island.* "Disease among dogs commenced in the fall and continued until about March. Some survived, but became blind."

\+ **18.** *Coppermine.* "Form of distemper, November to February. (1) Fatal to young dogs and pups in every case, after 10 days' sickness: (*a*) get thin around the loins, diarrhoea, listlessness, weakness in back, or in hind quarters, gradual loss of appetite; (*b*) in two or three days: complete loss of appetite, vomiting yellow matter, blood found in urine (some cases), death occurs two or three days later. (2) Dogs over four years old, recovered in many cases after quite a lengthy illness. Their symptoms started as (1*a*) then: running at eyes and nose, apparent difficulty in swallowing which lasts about four days (sore throat). Convulsions quite often."(2+, see Table 1.)

\+ *Coppermine.* "Disease among sledge dogs first made its appearance during the latter part of November, but appeared to have died out by the end of March. It was estimated that 75% of the dogs in this district died. The symptoms were loss of appetite, pus running from the eyes, vomiting, then death, sometimes within a few days, or not for several weeks."

\+ *Wilmot Island.* "Distemper January to March. Symptoms: (1) loss of appetite; (2) rubbing of eyes with paws followed in day or two by both eyes running pus; (3) dry, hot nose and excretion from nostrils; (4) loss of strength, desire for water, almost sure death in week or two. Seemed to affect white men's dogs worst. My own eight comparatively isolated but lost six of them—remaining two were not stricken. Natives not nearly so hard hit: on an average each lost about two dogs. I am of the opinion that the disease was brought from Coppermine.

There seemed to be an entirely different sickness amongst the natives' dogs—not so fatal but a very long sickness. Only symptoms of this: loss of appetite and strength, loose bowels and excretion of slimy matter and sometimes worms. Eyes not affected. This sickness apparent since last fall—long before any trace of the distemper. My own dogs not affected. All sickness and disease seemed to end in May."

\+ *Bathurst Inlet.* "An epidemic of distemper first made its appearance in November with the arrival of some natives to trade. Within a few days the next lot arriving to trade from an entirely different and isolated region were also noted to have the same sickness amongst their dogs. First symptom of disease was loss of appetite. In a few days, sometimes in a week or two, this was followed by pus running from the eyes. Some cases vomited, became increasingly weak, and died. If a dog could pass the initial stages and start eating again he sometimes recovered completely. However, if the eyes had been affected he usually went blind and had to be destroyed. In some cases also the dog was left with some part of his body he was unable to control, e.g. a hind leg, or his head jerking back and forth."

\+ *Perry River.* "Heavy loss of dogs due to sickness affecting the brain. Outbreak started in March and lasted until end of May."

\+ *Repulse Bay.* "Disease began locally about the middle of May. As there has been no report of the disease north of here and as the outbreak took place after the arrival of the Pelly Bay Natives, we presume that it was brought by them from the Western Arctic with which they are in contact. Mortality to the end of May was about 10% but by now (16 June 1939) it has

Table 3 (*continued*)

jumped to 50%. Symptoms: (1) refusal to eat, discharge at eyes and nose, weakness of the legs, then just lie around until death takes place; (2) foaming at the mouth, rushing around crazily, throwing fits and death during one of these sessions. Note: no loss of appetite in this case."

4. Large islands

+ *Fort Collinson.* "Disease first recorded in September when we lost two dogs. In late October and early November we lost three pups, about six weeks old. The natives' dogs were suffering from the same disease. Fresh teams came from Collinson Inlet and Hadley [Bay] but on their return trip started losing dogs. Natives from the west landed at Holman Island in September, so bringing the disease to that point. The disease had not reached Baillie Island when we left there in August. Symptoms: those of acute distemper. Many of the dogs commenced to stagger and there was a discharge of yellow pus from the eyes and in many cases the dogs turned blind. The percentage recovering was very low: in our case one in six. The native instances ranged from 20% to as high as 70–80%." (4+)

+ *Read Island.* "Outbreak from October until after Christmas: loss of appetite, discharge from eyes and nose, diarrhoea, general listlessness, moaning. About 90% of cases died. 50% of dogs caught disease. Many of those that recovered were blind but recovered their sight after a couple of months."

+ *Cambridge Bay.* "Dog disease broke out in Cambridge Bay area about end of February. Symptoms varied: blindness, general weakness, running at eyes and nose. About 75% mortality in teams which were infected. Disease was thought to have spread from the west."

+ *King William Island.* In March disease became epidemic, some families losing their entire teams. There was no trace of disease in the area until the arrival during March of travellers from Coronation Gulf, an area where disease was reported early in the winter. The symptoms were as usual except discharge from the nose more marked. (There was no trace of disease in white foxes.)"

+ *Fort Ross.* Disease broke out among sledge dogs in April having been brought into the country from Cambridge Bay where the disease had been prevalent earlier on in the winter. The disease was then later spread throughout the entire surrounding country destroying something like 80% of all the dogs at most points and some cases wiping them out altogether. Dogs were affected in two different ways: (1) There was a terrific discharge from the nose, and the eyes were affected, sometimes to the extent of blinding a dog completely. In a few instances dogs recovered from this form of the disease. (2) Animals affected with the other form did not recover. Dogs would suddenly become weak and unwilling to work, then after a while would vomit up clots of blood, finally lie down and die with a final discharge of blood from the nose and mouth."

+ *Arctic Bay.* "Disease broke out during the spring. The disease was carried from Fort Ross by visiting teams which had already got it from King William Island in a similar manner. There were two classes of disease: (1) Dogs contracted a swelling of the head and feet and pus formed. Animals became totally blind and died in a few days. (2) Dogs contracted a severe cold in the head (nose and eyes running) coughed continually and refused their food. Many of these dogs recovered after about three weeks."

+ *Pond Inlet.* "Epidemic disease amongst dogs, reported to have been brought from Western Arctic to Arctic Bay. Dogteams from Pond Inlet visiting Arctic Bay have been infected, though at this date [?31 May] the infection does not appear to be spreading to the other teams here. Symptoms: coughing, running nose, blood-coloured excrement. Death sometimes follows with suffocation or haemorrhage."

+ *Pond Inlet.* "The dog disease appeared in May among some dogs but not until July in the R.C.M.P. dogs, of which, by the end of August 1939 only 8 out of 14 were left. The employed natives of the R.C.M.P. lost 14 out of 16 and of the dogs belonging to other natives about 160 died out of 200. By September most camps had only two or three dogs left out of teams usually numbering 10–12. The Hudson's Bay Company lost 3 dogs out of 8. One was seen in convulsions on 5 September. The shortage of dogs throughout the country will add to the hardships to be expected anyway in the coming season." (Personal communication.)

Table 3 (*continued*)

Clyde River. "No apparent sickness amongst dogs, though there have been isolated cases of disease, probably due to malnutrition."

21. *Pangnirtung.* "This was a very poor hunting year for the Eskimos and a great majority of the dogs died of starvation."

Frobisher Bay. "Slight disease amongst dogs during March and April, diarrhoea and general weakness being the chief symptoms."

Hudson and James Bay (including posts on Quebec, Ontario and N.W.T. coasts).

+ *Moosonee.* "Most sledge dogs were affected by a disease diagnosed as 'false rabies' causing almost complete blindness and loss of the use of the limbs. The outbreak occurred in early December. Of the animals affected about 60% died."

+ *Moose Factory.* "An epidemic broke out during December and fully a score of dogs on Moose Island died. The dogs were seized with convulsions and died in a few hours. The epidemic appeared to be local as no sickness was reported from the east and west coasts of James Bay."

+ *Rupert House.* "Several dogs sick in March and April. About half of them died."

+ *Eastmain.* "Disease about end of April. Symptoms: loss of appetite, pus coming from eyes. Mortality among natives' dogs in some cases 100%; dogs owned by whites about 20%."

+ *Great Whale River.* "End of March and April six dogs were reported to have died and many sick from epidemic. Popular belief is that the sickness was contracted from the southern mail team from Moosonee while it stayed here for a few days in early March. The mail team was known to have sickness and some dogs had died before arrival here. This team had also been up the west coast of James Bay where it was also reported that dogs were dying from sickness."

+ *Attawapiskat.* "Disease occurred in January. It was brought up from Moose Factory by dogs. Five of our best dogs died and also several of the Indians' dogs. The symptoms were foaming at the mouth and a pus excretion from the eyes; also an entire lack of appetite. The Company dogs were well fed on seal meat and whitefish, but this did not seem to make any difference as all the best dogs died first. The disease seemed to be prevalent in this vicinity as several cases were reported inland." (2+)

Severn. "No epidemic. A few dogs have died but I believe from starvation."

10. *Eskimo Point.* "October to December. Slight indisposition: off feed and weakness."

Tavane. "Disease January to March. Symptoms: diarrhoea, no appetite for 7–10 days, almost too weak to stand. Mortality very low or none. Disease thought to have come from south."

+ **24**. *Chesterfield Inlet.* "January to March: general weakness, diarrhoea, seemed to derive no nourishment from food (although good appetites in early stages) as they were continually vomiting. After 2–3 days would not eat at all; then after a few days would start to eat again. The usual signs of distemper were not present; there were no signs of worms. No dogs died from this disease. Sickness lasted about two weeks in each dog; but not all were affected at the same time, some not at all. Dogs affected on trips had to be carried on sledge."

+ *Chesterfield Inlet.* "Sickness first reported in February. There was severe diarrhoea, loss of appetite and strength. About 5% died. Within two weeks the animals started to recover, and within the following week were able to work."

+ *Chesterfield Inlet.* "Although only of short duration and involving no known deaths this epidemic of dysentery among the dogs came at a bad time and seriously inconvenienced the natives in the fox and cariboo hunts. Symptoms: running nose, very violent diarrhoea and complete prostration. It was impossible to make the dogs stand up, even in harness." (Personal communication.)

4. SUMMARY

1. Over 95 observers have contributed information on population trends in wild life in the Arctic and Subarctic.

2. Lemmings (*Lemmus, Dicrostonyx*) decreased nearly everywhere in the Eastern Arctic; but there were regional exceptions, notably in Northern

Labrador and at Whale River and Fort Chimo. North and north-west of Hudson Bay recovery was in progress after an earlier decrease in lemmings. A peak may have been reached on the west coast of Victoria Island.

3. Arctic foxes (*Alopex lagopus*) declined sharply in most of the Eastern Arctic after two years of fairly general increase. In much of the Western Arctic, but excepting King William Island and the coastal mainland, increased fox populations were experienced.

4. Snowy owls (*Nyctea nyctea*) in the Eastern Arctic mostly reached and, in places, passed a peak during 1936–38. Decrease was general in 1938-39 except in Northern Labrador and north and north-west of Hudson Bay. In 13 out of 17 regions where snowy owls were increasing during the year an increase in lemmings was also noted.

5. Sledge dog teams have suffered severely through "distemper". The consensus of opinion is that the disease was spread eastwards by contact between teams.

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THE BIOLOGY OF THE SMALL WHITE BUTTERFLY (*PIERIS RAPAE*), WITH SPECIAL REFERENCE TO THE FACTORS CONTROLLING ITS ABUNDANCE

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A. GENERAL BIOLOGY

1. Introduction

The present work was undertaken primarily as a study of the fluctuations in numbers of an insect species. The small white butterfly, *Pieris rapae* (L.), was chosen for study because it was a large insect whose general biology was already fairly well known. As it turns out, it is not a particularly favourable insect for the study of fluctuations in numbers. The adult is so mobile (partly migratory) that such a study should be made over a large area to give significant information. The present work was carried out almost entirely on the grounds of the Imperial College Biological Field Station, Slough, Buckinghamshire. These grounds include about $12\frac{1}{2}$ acres, more than half of which are cultivated. When the work started, much of the surrounding land was agricultural and much cabbage was grown; more recently it has largely been given over to building. The present work does not justify any wide generalization about the factors controlling the abundance of *P. rapae*. It is hoped, however, that some of the methods evolved may be of value to those engaged in similar studies; there is, further, a good deal of new information about the biology of the butterfly.

2. The characters distinguishing allied species

The three common British Pierines are the small white (*P. rapae* (L.)), the large white (*P. brassicae* (L.)) and the green-veined white (*P. napi* (L.)). The adults are easily separated by means of the coloured illustrations in various well-known books. Of the other British Pierines, only two have larvae which feed on Cruciferae and likely therefore to be found with those of *Pieris*. The Bath white (*Pontia daplidice* (L.)) is a scarce immigrant and need not be considered. The orange-tip (*Euchloe cardamines* (L.)) is, of course, very distinct in the adult stage.

The eggs

P. rapae and *P. napi* lay their eggs singly (see also p. 246) on the food plant. According to Frohawk (1924), there are 12 longitudinal ridges on those of *P. rapae* and 14–15 on those of *P. napi*. *E. cardamines* also lays its eggs singly but soon after laying they become orange instead of yellowish green; they have about 18 keels. *P. brassicae* lays its eggs in groups of 30 or more; they have 17–19 keels.

The larvae

The larvae of *P. brassicae* are very distinct with their characteristic, mottled, green and black colour pattern; moreover, they are gregarious. The larval instars have not been fully studied but it is not difficult to recognize them by size, especially of the head, alone. The first two instars have the head entirely black; the third has the clypeus yellow but the rest of the head black. In the fourth and fifth instars, besides the yellow clypeus, there is a greenish yellow, dark-mottled area behind each eye. Apparently the instar at which these colour changes take place is not absolutely fixed. I have seen one larva with an entirely black head which seemed, by its size, to be in the fourth instar.

The larvae of *P. rapae* and *P. napi* are very alike, though those of *P. napi* are rarely found on cabbage (see p. 245). As a result of personal studies and of some preliminary observations made by Mr J. F. Perkins, the following distinguishing characters are available. Those for separating the instars are also indicated.

Table 1. *Instars of* P. rapae *and* P. napi

	P. rapae		*P. napi*
Stage	Head width in mm., mean of 10 individuals (J.F.P.)	General characters	Distinguishing characters
I	0·417	Body with only primary setae; those of head partly black	Head setae all pale
II	0·643	Secondary setae present; no dorsal yellow line	Not certainly distinguishable
III	0·972	Dorsal yellow line incomplete behind	No dorsal line
IV	1·498	Dorsal line complete	—
V	2·259	—	—

With a little experience, the stages of *P. rapae* can be distinguished merely by size and head width, estimated by eye alone. *Euchloe cardamines* has a larva rather resembling that of *P. napi*, but it is considerably more mottled with white, especially on each side. The larva is also relatively longer and thinner and tapers at each end.

The pupae

P. brassicae pupa is quite distinct by its large size and close, green, black and yellow mottling. *Euchloe cardamines* has a peculiar long, narrow, pointed pupa, quite unmistakable. *P. rapae* and *P. napi* are rather similar but may be distinguished by examining the proboscis sheath. In *P. rapae*, this projects far beyond the antennal sheaths, in *P. napi* only a very short distance.

The sexes of the pupae are easily distinguished. Both sexes have a small pit at the centre of sternite IX. The female has, in addition, an impressed line at the centre of sternite VIII.

3. Food plants

P. rapae. Eggs or larvae have been found on cabbage (*Brassica oleracea*), swedes (*B. campestris* var.), turnip (*B. campestris*), mustard (*B. nigra*), sea-kale (*Crambe maritima*), garlic mustard (*Sisymbrium alliaria*), hedge mustard (*Sisymbrium officinale*), horse-radish (*Cochlearia armoracia*), hairy bitter-cress (*Cardamine hirsuta*) and nasturtium (*Tropaeolum majus*). A number of other food plants are recorded in the literature; the only abundant Crucifers at Slough on which eggs have never been found are shepherd's purse (*Capsella bursa-pastoris*) and wallflowers (*Cheiranthus* spp.).

P. napi. Eggs or larvae have been found on cabbage very rarely,[1] garlic mustard, hedge mustard, hairy bitter-cress, water-cress (*Nasturtium officinale*) and cultivated stock (*Matthiola* sp.).

P. brassicae. Eggs or larvae have been found on cabbage, swedes, horse-radish, *Tropaeolum* and dame's violet (*Hesperis matronalis*).

E. cardamines. Larvae have been found on garlic mustard, dame's violet and large bitter-cress (*Cardamine amara*).

In the late summer of 1932 an investigation was made into the relative importance of the various food plants of *P. rapae.* Table 2 shows the result of this inquiry. The more important plants in the Slough grounds are cabbage, swedes, garlic mustard, hedge mustard, horse-radish and *Tropaeolum.* Probably, far more eggs are laid on cabbage than on any other plant.

The comparison of the numbers per plant can only be taken as very rough. As will be shown in a later paper, the situation in which the plant is growing has a large effect on the amount of oviposition. Further, the eggs and young larvae are far more destroyed by predators on the wild Crucifers than on cabbage.

[1] Out of 112 eggs found on cabbage and kept for hatching, all produced *P. rapae.* Out of more than 3000 larvae found on cabbage, only five belonged to *P. napi.*

The number of eggs on *Sisymbrium officinale* and *Tropaeolum* was deceptively high. Favoured plants of *Sisymbrium* or plants growing in a certain relation to the surrounding vegetation are liable to have many eggs laid on them. Other plants have few or none. It is difficult at present to compare the attractiveness of different plants. The same is true, to a less extent, of *Tropaeolum*. In August 1934, 134 plants of *S. officinale* were examined and only four eggs and two larvae were found.

Table 2. *Relative importance of food plants of* P. rapae

Plant	No. of plants examined	Date (August)	Plants without eggs or larvae	Plants with eggs or larvae	No. of eggs and larvae	No. per plant
Cabbage	100	16	60	40	57 eggs, 10 larvae	0·67
Swedes	100	19–22	69	31	4 eggs, 27 larvae	0·31
Sea-kale	100	23	74	26	17 eggs, 12 larvae	0·29
Turnip	50	18	47	3	4 larvae	0·08
Mustard	50	18	49	1	1 dead larva	0·02
Tropaeolum majus	100	15	52	48	52 eggs, 29 larvae	0·81
Sisymbrium alliaria	103	18	88	15	8 eggs, 3 larvae	0·10
Sisymbrium officinale	54	16	32	22	41 eggs, 15 larvae	1·04
Capsella bursa-pastoris	50	17	50	0	—	—
Cardamine hirsuta	50	17	49	1	1 larva	0·02
Horse-radish	12 leaves	17	1 leaf blank	—	17 eggs, 48 larvae	—
Water-cress	50	19	50	0	—	—

Although eggs are quite frequently laid on sea-kale, it is apparently an unsuitable food for the larva. Only rarely have larvae of any size (third stage) been found and all attempts to rear the larvae on it failed. Of twenty larvae, 18 died in the first stage and none pupated. *P. brassicae*, however, feeds on it quite successfully.

The turnips referred to in Table 2 belong to a variety with hairy leaves. Apparently this acts as a deterrent to oviposition and probably smooth-leaved varieties would be laid on freely. There are many references in the literature to larvae attacking turnips.

The question as to how oviposition is determined is a very complex one on which a separate paper will be published in the future. At this stage data will be given only of the position of the egg on the plant. In egg laying, the female characteristically holds on to the edge of a horizontal leaf and bends her abdomen beneath it to lay an egg a little way from the margin. If the leaf is vertical, she may cling to an outstanding vein on the disk of the underside. Similarly, in a folded leaf, eggs may be laid on the upper side. Rarely two eggs have been found side by side (see below) and probably these were laid consecutively. Normally, after oviposition (e.g. in a cage) a female flies for some time before laying again. During 1932–36, the positions of 1546 eggs were recorded: 1334 were on the underside and 212 (13·7%) on the upper side. Out of the 1546 eggs, the following examples of two or three eggs situated side by side (probably laid consecutively) were observed: one case of three eggs (underside), nine cases of two eggs (underside), two cases of two eggs (upperside).

On narrow-leaved plants, such as hedge mustard, the position is less fixed and almost as many are laid on the upperside as on the underside; many are also laid on the stalk.

4. Life history and number of generations

Life history

A small-scale investigation was made of the length of the life history under controlled temperature conditions. The eggs and larvae were kept in glass-topped tins and given fresh cabbage every day.

Table 3. *Life history of* Pieris rapae

Temperature °C.	No. of eggs	No. of eggs hatched	Incubation period (days)	No. of larvae	Larval period (days)	No. of pupae	Pupal period (days)
7	17	5	26–29 (27·6)		All larvae died in 2–3 days		
12	27	19	8–11 (9·7)		All larvae died within 28 days		
17	27	24	6	24	17–22 (20·2)	16	10–13 (11·0)
22	27	25	4–5 (4·7)	28	12–16 (13·4)	20	8–10 (8·35)
27	65	65	3–4 (3·7)	14	11–14 (11·6)	13	6–7 (6·5)
30	25	Most	2·5 (approx.)	—	—	—	—
32	26	All shrivelled	—	—	—	—	—

The figures in brackets are means.

It will be seen that development of the eggs is possible between 7° C. and about 30° C., but that the larvae cannot develop satisfactorily except at some temperature above 12° C. There appears to be very little difference, under the conditions of these experiments, between the developmental periods of males and females, though under field conditions males usually appear a few days before the females in each generation.

The larva has four moults and five instars and a few observations were made on the length of the instars under laboratory conditions.

Table 4

1932. Laboratory conditions, mean temperature 19·2° C. (22♂, 17♀)

Instar	I	II	III	IV	V (Feeding)	V (Resting before pupation)
Duration in days: range	2·5–6	1·5–5	2–5	3–6·5	4–14	1–4
mean	4·5	3·0	3·3	4·1	6·0	1·8

A similar set of data for *P. brassicae* are perhaps worth recording.

Table 5

1933. Laboratory conditions, mean temperature 15·7° C. (8♂, 4♀)

Stage ...	I	II	III	IV	V (Feeding)	V (Resting)
Mean duration (days)	6·5	3·58	2·9	3·17	5·83	1·66

Before pupating, the larva ceases feeding and there is a wandering phase. Finally, it settles down, spins a silken platform, becomes shorter with the posterior end more pointed, and turns into a pupa. Just before pupation, a single lump of reddish or brownish excreta is passed. Dissections of the late fifth instar larva show that just before pupation the Malpighian tubules become reddish and this is probably the source of the red matter in the excreta. The inner section of fat body also becomes opaque white instead of semitransparent.

There appears to be a difference between the broods in the extent of the wandering phase, so that in the first brood many pupae are found on the cabbages whereas in the later broods only a few (as recorded, also, by Moss, 1933).

Table 6. *Cabbages examined each year for larvae and pupae*

Generation	Dates	No. of larvae	No. of pupae	Pupae as % of larvae
I	23–30 June 1933	358	98	21
I	18–22 June 1934	45	10	18
I	27 June–18 July 1935	148	20	14
I	8–18 June 1936*	90	1	1
II	23 July–31 Aug. 1934	66	4	6
II	19 July–31 Aug. 1935	121	2	2
II	20 July–3 Aug. 1936	42	2	4
III	5 Sept.–28 Oct. 1933	113	3	3
III	1 Sept.–11 Oct. 1934	215	2	1
III	2 Sept. –16 Oct. 1935	278	1	0·4
III	1 Sept.–4 Oct. 1936	478	2	0·4

* It was necessary in 1936 to cease collecting before the majority of larvae had had time to pupate.

The actual percentage of pupae found depends, of course, on the date of examination, if the latter is not continuous. Nevertheless, the trend of the above figures is unmistakable.

I have not made any study of the biology of the adult, but Norris (1935), using some of my material, published data on the longevity and on the number of eggs laid by females fed on cane sugar and water and kept in cages.

Table 7

Data from Norris (1935)

Sex	No. of specimens	Mean no. of eggs laid	Mean no. of eggs ripened	Mean longevity (days)
Female	6	356	487	19·8
Male	10	—	—	23

These figures are minima since cage conditions are not altogether suitable for the butterflies. If not fed, the adults soon die and the females lay very few eggs.

From various sources (collections of larvae, experimental larvae, a few small collections from Hampshire, Kent and Cambridgeshire) 1149 adults were bred, 550 male, 599 female, sex ratio 1 : 1·09. Of 417 pupae which died, 221

were male and 196 female. Thus the sex ratio of those that died was 1 : 0·887 and the total pupal sex ratio was 1 : 1·031. The difference between the sex ratios of those that died and those that emerged is just significant (P between 0·05 and 0·02). The other differences are not significant.

Number of generations

The information on this subject in the British literature is very misleading. It is usually stated that there are two generations with sometimes a partial third. In 1934, when continuous observations were first made, it was found that there were three complete generations and this is evidently the normal state of affairs. In most years there is also a partial fourth generation. In 1932, under laboratory conditions, fifth and sixth generations (the latter in the middle of December) were obtained.

The primary observations on the number of generations consisted of egg counts on a sample row of cabbages. About 80 plants (sometimes a few died in the course of the summer) were examined twice a week and all eggs found were marked with a ring, made by pressing an object such as a pencil cap or top of a fountain pen against the leaf. This ring, surrounding the egg, is a permanent mark which enables "new" eggs to be distinguished from those marked in previous examinations. When the egg hatches, the ring can be torn out of the leaf. The record of the oviposition rate forms one of the best pictures of the seasonal history of the species.

The following points may be noticed in the records in Table 8:

(1) Oviposition in the spring may begin on any date between 29 April and 1 June, usually between 1 and 10 May.

(2) The oviposition of the first generation stops between 18 June and 29 June.

(3) The pause in the oviposition cycle on 27 May 1935 is probably due to the low temperature of the week ending 20 May 1935 (see p. 262). There is no obvious reason for the similar pause on 28 May 1936.

(4) There is about a fortnight between the end of the first oviposition period and beginning of the second, which extends approximately from 9 July to 9 August. There may or may not be a clear interval between the second and third periods.

(5) The third oviposition period extends from 9 August to a rather indefinite date at the end of September or in the middle of October. In 1933 and 1935 there are subsidiary maxima in September (4 Sept. 1933, 26 Sept. 1935). These are not obviously accounted for by variations in weather, but (at least in 1933) are probably due to the emergence of a partial fourth generation (see p. 252).

(6) The relative amounts of oviposition during the three periods are as follows:

	Generation		
Year	I	II	III
1934	51	102	318
1935	57	>61	117
1936	145	25	94

The reduction oviposition during the last two generations of 1936 was probably largely due to the number of cabbages which had been attacked by club root (*Plasmodiophora*) and so made less attractive, as noted in the footnote to Table 8.

Table 8. *Egg counts on* 80 *plants*, 1934–36

Generation										
	1934									
I	Week ending	—	17 May	24 May	31 May	7 June	14 June	21 June		No examinations from 22 June to 8 July
	No. of new eggs	14 May, 4 eggs present	7	4	8	17	8	3		
II	Week ending	—	12 July	19 July	26 July	2 Aug.	9 Aug.	16 Aug.		No new eggs between 6 Aug. and 16 Aug.
	No. of new eggs	9 July, 5 eggs present	14	28	27	25	2	0		
III	Week ending	—	23 Aug.	30 Aug.	6 Sept.	13 Sept.	20 Sept.	27 Sept.	27 Sept.–1 Oct.	
	No. of new eggs	20 Aug., 5 eggs present	9	54	60	108	68	10	4	
	1935									
I	Week ending	—	13 May	20 May	27 May	3 June	10 June	17 June	24 June	
	No. of new eggs	6 May, 4 eggs present	17	11	2	16	1	4	2	
II	Week ending	—	1 July	8 July	15 July	22 July	29 July			No. examinations from 30 July to 21 Aug.
	No. of new eggs	—	0	2	18	20	21			
III	Week ending	—	29 Aug.	5 Sept.	12 Sept.	19 Sept.	26 Sept.	3 Oct.	10 Oct.	
	No. of new eggs	22 Aug., 4 eggs present	13	14	32	14	20	9	11	
	1936									
I	Week ending	—	14 May	21 May	28 May	4 June	11 June	18 June	25 June	
	No. of new eggs	7 May, 3 eggs present	12	19	13	47	37	14	0	
II	Week ending	—	2 July	9 July	16 July	23 July	30 July	6 Aug.		
	No. of new eggs	—	0	1	0	2	17	5		
III	Week ending	—	13 Aug.	20 Aug.	27 Aug.	3 Sept.	10 Sept.	17 Sept.		On 21 Sept. only one additional egg present*
	No. of new eggs	—	48	24	10	8	1	3		

Partial observations for 1932–33

Generation										
	1932									
I	Week ending	—	30 May	6 June	13 June	20 June	27 June			29 June only one additional egg present. Adults of new generation seen on 14 July
	No. of new eggs	—	0	17	20	34	10			
	1933									
I	Week ending	—	6 May	13 May	20 May	27 May	3 June	10 June	17 June	22 June only two additional eggs present. Adults of new generation seen on 1 July
	No. of new eggs	29 April, 5 eggs present	8	25	25	47	59	35	8	
III	Week ending	—	7 Aug.	14 Aug.	21 Aug.	28 Aug.	4 Sept.	11 Sept.	18 Sept.	25 Sept. 2 Oct.
	No. of new eggs	—	8	25	50	29	124	67	12	15 8

* Observations were stopped on 21 September because it was evident that the cabbages were no longer attractive (probably owing to club-root) Sixty cabbages on another plot were examined on 22 September and found to bear 27 eggs (twelve times as many).

5. Hibernation and pupal diapause

All the Pierines studied pass the winter as a pupa and probably none of the other stages is capable of an extended diapause. There are records in the literature (e.g. Frohawk, 1936: *P. brassicae*) of larvae being found in December or January; but these are rare laggards which have been forced to develop slowly by the cold weather and there is little evidence that they pass through the winter without pupation.

In *P. rapae*, the larvae of the first generation almost universally give rise in a few weeks to the adults of the second generation. I have a record of a fifth-stage larva collected on 12 June 1936 which produced a female on 26 May 1937 and a fifth-stage larva collected 28 June 1933 which emerged 2 December 1933 (indoors). I have also one record of a first-stage larva collected 31 May 1935 which pupated 24 June and produced a male on 15 May 1936. There was also one fourth-stage larva collected 19 June 1935 which pupated 28 June and produced a male during the first three weeks of August (i.e. skipping the second generation and emerging in the third). No experiments, however, with low temperatures have been performed to determine whether first generation larvae are regularly capable of producing dormant pupae.

The larvae of the second and third generations produce an increasing number of dormant pupae as the season progresses, till, finally, at the end of the season, all the pupae formed, even if kept warm, refuse to emerge without a diapause. Unfortunately it is difficult to exhibit the facts clearly. Larvae collected in the field are found in all stages and have been subjected to field conditions for varying periods. In the laboratory, although there is no temperature control, extremes of temperature are avoided.

Thus, larvae belonging to the first and fifth instar when they pupate will have been exposed to laboratory conditions for very different periods. If one were to deal only with larvae of a particular stage, the numbers would be so cut down that it would be difficult to obtain significant figures. Two different types of table have been prepared, which together give most of the relevant information. A special column will be found for what is termed the "mean stage"; by assigning the egg the value 0, the larvae the values 1–5 corresponding to the instar, and the pupa the value 6, it is possible to obtain an average value for the state of development of a mixed collection of larvae; this average value is termed the "mean stage" of the collection.

The irregularities in the numbers of the two preceding tables are due to a number of causes, principally the following: (1) Larvae were not collected in equal numbers every week; occasionally none were collected (e.g. during holidays such as 7–21 August 1935). (2) The number killed off by parasites or which died of disease varied greatly in different collections. The above tables are based entirely on specimens which reached the adult stage.

Table 9 shows how larvae of the second and third generations produce an

increasing number of dormant pupae. Moreover, the emergent individuals are on the whole those which were removed from field to laboratory conditions at an early stage, for in 10 out of 13 comparisons the mean stage of emergent individuals is lower. There is, however, no detailed regularity in this relation. There is again a loose connexion between the seasonal fall in temperature and the increase of dormancy, but it is impossible as yet to fix a date or a temperature at which dormancy becomes universal.

Table 9. *Emergence and dormancy of* Pieris rapae *collected at different dates during the summer*

Year and dates	Temperature ° C.			No. collected	Emergent			Dormant			% dormant
	Mean weekly	Weekly max.	Weekly min.		♂	♀	Mean stage	♂	♀	Mean stage	
15 Aug.–19 Aug. 1932	19·0–20·8	34·0	12·2	63	29	32	0·9	1	1	1·5	3
21 Aug.–17 Sept. 1932	20·8–15·0	21·1–25·0	5·5–10·0	20	4	6	4·4	3	7	3·7	50
8–29 Aug. 1933	20·0–17·2	26·1–31·1	8·3–10·0	38	19	19	2·9	0	0	—	0
1–12 Sept. 1933	19·0	26·6–29·0	9·0	26	12	6	3·1	5	3	4·4	31
17–30 Sept. 1933	15·0–14·0	20·0–23·3	5·5– 9·0	8	2	4	2·3	2	0	3·0	25
2–28 Oct. 1933	15·0– 9·4	13·3–20·0	2·2– 9·0	25	1	1	3·5	16	7	4·9	92
31 May–26 July 1934	13·3–18·3	22·2–29·0	2·2– 8·3	35	11	24	3·5	0	0	—	0
31 July–7 Aug. 1934	16·6	25·5	5·0	108	33	57	3·3	8	10	3·2	17
8–15 Aug. 1934	15·5	22·2	10·0	43	9	19	3·9	4	11	4·1	35
16–23 Aug. 1934	16·1	25·5	7·2	36	11	6	4·4	11	8	4·5	53
24 Aug.–10 Oct. 1934	11·1–16·6	17·2–26·6	2·2– 7·2	67	0	0	—	33	34	4·6	100
27 May–21 July 1935	12·2–21·1	17·7–29·0	2·2–10·0	103	54	48	4·1	1	0	1·0	1
22 July–6 Aug. 1935	14·4–18·3	22·8–25·0	4·4– 9·0	15	8	3	2·3	3	1	4·0	27
7–21 Aug. 1935	15·5–19·4	22·2–29·0	6·6	0	—	—	—	—	—	—	—
22–29 Aug. 1935	17·7	30·5	10·0	21	1	3	4·7	8	9	3·9	81
30 Aug.–16 Oct. 1935	9·0–14·4	14·0–24·4	0·5– 5·5	25	2	0	0	11	12	3·75	92
10 June–4 Aug. 1936	14·0–17·2	17·2–23·3	8·3–14·0	35	19	15	4·4	0	1	5·0	3
5–20 Aug. 1936	14·4–15·5	21·1–22·2	7·7– 9·4	22	3	8	3·3	7	4	3·7	50
21 Aug.–5 Sept. 1936	16·1–17·2	20·0–26·1	6·6–11·7	51	2	9	3·1	21	19	4·35	78
6–29 Sept. 1936	12·8–14·4	19·0–20·5	5·0– 9·0	75	0	0	—	47	28	4·7	100

Admittedly the screen temperatures recorded are only very roughly correlated with those of cabbage leaves where the larvae live. It is also evident that temperatures which are associated with dormancy in the late summer are insufficient to cause dormancy amongst larvae of the first generation in May and June. In each year there is usually a date after which 80–100% of the larvae become dormant; in 1933–36, these dates were 2 October, 24, 22, 21 August. In the same years, the lowest mean weekly temperature and the absolute screen minimum for the first three weeks of August were 17·2 and 8·3° C., 15·5 and 5·0° C., 14·4 and 4·4° C., 14·4 and 7·7° C. This again suggests that in 1933 there was a considerable emergence of a fourth brood (cf. p. 249) owing to the slightly warmer weather. In 1934–36, the percentage of pupae emerging after 24, 22 and 21 August respectively was 0, 13 and 9. Perhaps the 13% in 1935 accounts for the secondary September peak in oviposition (cf. p. 249).

These suggestions are supported by the different analysis of the same data given in Table 10. The probable limits of the pupation of the second and third generations have been indicated; in 1936 there was apparently no sharp

Table 10. *Emergence and dormancy of pupae of* P. rapae *during the summer*

		June		July					August				September					October				November
Week ending	Year	17	24	1	8	15	22	29	5	12	19	26	2	9	16	23	30	7	14	21	28	4
Weekly min. temp. ° C.		4·0	5·5	9·0	6·6	10·6	7·7	7·7	10·6	9·4	9·0	11·1	6·1	5·5	10·0	4·4	2·2	—	—	—	—	—
Generations	1932				I									III								
No. pupating in that week		0	0	7	5	28	33	0	0	0	0	8	24	47	5	1	0	—	—	—	—	—
% dormant		—	—	0	0	0	0	—	—	—	—	0	33	4	20	100	—	—	—	—	—	—
No. adults emerging in that week		0	0	0	0	8	7	23	33	2	0	0	0	7	8	37	10	—	—	—	—	—
Weekly min. temp. ° C.		6·1	7·2	8·3	12·2	10·0	10·0	11·1	9·4	11·7	9·0	8·3	9·0	9·0	5·0	9·0	10·0	5·5	4·4	2·8	2·2	5·5
Generations	1933		I								II							III				
No. pupating in that week		2	14	21	0	0	0	0	0	4	12	4	0	14	18	3	6	4	9	8	8	6
% dormant		0	0	5	—	—	—	—	—	0	0	0	—	21	11	0	33	0	55	100	100	83
No. adults emerging in that week		0	0	2			33		0	0	1	8	7	2	1	3	4	4	0	0	1	0
Weekly min. temp. ° C.		4·0	6·6	6·6	9·0	8·3	8·3	10·0	5·0	10·0	8·3	3·3	3·3	5·5	3·3	2·8	2·8	2·2	2·8	0·5	1·0	
Generations	1934	I									II							III				
No. pupating in that week		8	0	0	0	0	0	20	45	73	26	35	15	0	3	4	7	14	22	14	1	
% dormant		0	—	—	—	—	—	0	6·6	23	36	54	33	—	100	100	100	100	100	100	100	
No. adults emerging in that week		0	0	8	0	0	0	0	0	3	15	46	45	43	8	0	0	0	0	0	0	
Weekly min. temp. ° C.		7·2	10·0	9·0	6·6	9·0	6·6	9·0	4·4	6·6	6·6	10·0	4·4	3·3	5·5	5·5	1·0	1·0	0·5	−4·0	−2·2	
Generations	1935			I						II							III					
No. pupating in that week		1	4	34	38	12	0	0	2	8	2	0	9	12	14	7	7	6	7	1	2*	
% dormant		0	20	0	0	0	—	—	0	12·5	0	0	66	100	93	100	100	83	100	100	50	
No. adults emerging in that week		0	0	1	22	42	22	0	0	1	4	5	2	0	3	0	1	0	0	1	0	
Weekly min. temp. ° C.		9·0	9·0	12·2	14·0	12·2	11·1	8·3	10·0	10·6	9·4	7·7	6·6	11·7	8·3	9·0	3·3	−1·0				
Generations	1936		I								?II				III							
No. pupating in that week		19	11	0	0	0	0	0	0	0	6	8	26	30	24	28	13	14				
% dormant		0	9	—	—	—	—	—	—	—	83	25	73	73	96	100	100	100				
No. adults emerging in that week		0	0	25	2	2	0	0	0	0	0	0	3	7	4	8	1	0				

* One emerged 1–21 November 1935.

separation but not many larvae of the second generation were collected in that year. In 1934 and 1936, there was only a single, compact autumn emergence of adults in the laboratory. In 1933 and 1935, the laboratory emergence took place over a much longer period and went on later. Clearly in these years, as suggested before, there was a partial fourth brood.

Not enough data are available to show whether there is a special sensitive stage for the induction of dormancy. The fact that the only emergent individuals out of 25 collected between 30 August and 16 October 1935 were bred from the egg perhaps suggests that this stage is insensitive. It has already been shown (p. 249) that a fifth and sixth generation can be bred under laboratory conditions, so there is certainly no obligate diapause.

B. METHODS OF ESTIMATING POPULATION DENSITY

6. General considerations

It is very much more difficult to estimate the numbers of terrestrial animals than it is of marine animals. Of terrestrial animals, the subterranean ones are the easiest to deal with by a standard method of sampling, though the actual technique is very much more laborious than that for dealing with aquatic forms. Animals which live in the herbage layer can be collected by sweeping with nets and, with precautions, some estimate of their numbers can be obtained. The Lepidoptera present a rather special problem; they are too mobile and also not really sufficiently abundant to be dealt with adequately by any mechanical method of sampling. The normal method of estimating the population density of such insects is to make counts of a particular stage in the life history, by careful search on sample plots. Apart from the labour involved, there is no reason why this method should not give satisfactory results, provided certain precautions are taken. First, the stage to estimate should be the adult or the egg, since the checks on the species have operated at this point for a much shorter period than on any larval stage. Fluctuations in larval numbers might be due either to fluctuations in the numbers of the species or to variations in the intensity of the checks in that generation; fluctuations in adult or in egg number are more likely to be due to the first cause alone. As a rule, and in *Pieris* in particular, the eggs are much more easily counted than the adults.

Secondly, it is necessary to have a series of sample plots which will give a real measure of the abundance, a measure that is whose accuracy can be assessed statistically. The general methods for the lay-out of sample plots in agricultural experiments have been explained in a number of recent works but it was soon found that the study of a mobile insect involved quite special difficulties. The standard agricultural techniques are devised to meet the problem of semi-permanent local differences in soil fertility. The experimental material (plants) is non-mobile and the methods enable effects due to the local

variations in the soil to be distinguished from those due to special treatments (e.g. manures). When studying *Pieris*, however, it was found that although semi-permanent local differences might (acting through the plant host) have some effect on the number of eggs laid, the main disturbing factor was the active choice of oviposition site by the insect and this might be determined to a considerable extent by the whole nature of the territory surrounding the sample plots.

A detailed discussion of this problem will be given elsewhere in a study of the factors determining oviposition. But it may be stated here that the paths taken by *Pieris* in flying over a small area (5–10 acres) may be determined by the nature of the vegetation (particularly, perhaps, the number of flowers) in a much larger surrounding area. The effects so produced could not be controlled since even on the area studied only the vegetation of the sample plots themselves could be kept constant. Moreover, the relation of the time of flowering of such plants as thistles to the course of a *Pieris* generation differed from year to year and was uncontrollable. As a result, the variation in egg number from year to year or from plot to plot was quite as much a measure of attractiveness of the plots as of the numbers of the insects.

Until the exact nature of the attraction is better understood, it is impossible to analyse the counts on separate plots to obtain a measure of the accuracy of the estimation of population density. It has been concluded, therefore, that the egg counts actually made are more valuable as material for the study of choice of oviposition site than as an indication of seasonal variation in numbers. A brief account of the actual estimates of density obtained is given in the next section.

7. Egg counts

The methods of marking and counting eggs have already been described (p. 249). The following technique was adopted as standard. The cabbages were grown on a series of plots "S" in the front field at Slough. Only half the plots were occupied, the other half being occupied by mycological experiments. Very little control could be exercised over the vegetation of the surrounding plots. The cabbage plots were in a row (1–14) from west to east and consisted each of 24 cabbages, arranged in four rows of six (six along the E.-W. line). The third row of six in each plot was examined twice a week (Monday and Thursday). In 1932 only the first generation was studied and this on a different set of plots. In 1933–36, the plots "S" were used, but in 1933 the second generation was not kept under observation.

A thorough search was made of every leaf. It is probable that a few eggs are overlooked either entirely or for one or more examinations after their first appearance. A few are also accidentally brushed off in the course of manipulating the leaves. A certain number were actually seen to have been brushed off (38 out of 1337, 2·8%); probably the number unknowingly lost

was about the same. There is an indirect method by which the number of eggs overlooked or brushed off after marking can be estimated. If an egg is not found until after two or more examinations, its apparent incubation period will be too short. In the same way, if an egg was brushed off before it hatched, its apparent incubation period would be reduced. A study of the apparent incubation period has been made for all eggs observed in 1934. If an egg was first observed on, say 7 May (not having been there on 5 May) the date of laying was taken as 6 May. A date for hatching was similarly obtained midway between the last date the egg was seen and the first on which it was absent (only about one-quarter of the eggs were actually seen to hatch). This apparent incubation period would agree fairly closely with the real one if the periods of a considerable number of eggs were averaged. The apparent incubation period can be compared with the actual one (Table 3) at a constant temperature the same as the mean screen temperature for the period in question. Table 11 gives the data for 1934; periods with identical mean screen temperatures have been grouped together. The method is very rough but it is certain that if many eggs were being overlooked or brushed off after marking, the apparent incubation period would be distinctly shorter than the real one. It will be seen from the table that the agreement is pretty close on the whole. (Compare also p. 259 and Table 13.)

Table 11. *Apparent incubation period of* Pieris *eggs in field*

Mean screen temperature °C.	Duration of egg stage in days					No. of eggs observed	Mean duration	Laboratory duration at same constant temperature
	3·5	7	10·5	14	17·5			
12·8	19	37	1	1	—	58	6·0	9·1
13·3	2	2	16	12	—	32	11·1	8·7
13·9	7	8	7	1	—	23	7·3	8·3
15·0	9	18	26	3	—	56	7·9	7·5
15·5	—	6	—	—	—	6	7·0	7·1
16·6	27	71	6	1	1	106	6·5	6·3
17·2	12	16	—	—	—	28	5·5	6·0
18·3	13	16	—	—	—	29	5·4	5·7

Table 12 gives the numbers of eggs observed in each generation of 1933–36 (except the second on 1933) together with the number of larvae and pupae collected in these years. The amount of time spent in searching for larvae in different years was not identical but the figures are probably roughly comparable. The number of larvae and pupae discovered is in some ways a less sensitive index of abundance since it partly reflects the abundance of predators and also of those parasites which kill the larva before it reaches maturity. Only one insect parasite is known to do this at Slough but there may also be deaths from protozoal diseases or wilt or due to climate. Moreover, most of the pupae are too well hidden to be found. On the other hand, the larvae were collected from many more cabbages and their numbers are not so much affected by the relative attractiveness of a particular plot. Since the larvae and pupae were collected from repeated searches of a larger number of cabbages, their

abundance is expressed as a percentage of that of the eggs in the corresponding generation.

Table 12. *Number of* P. rapae *deduced from egg counts compared with number of larvae and pupae collected*

Year	Generation	I	II	III	Mean % larvae and pupae
1933	No. of eggs	82	?	552	
	Larvae and pupae %	641	—	69	355
1934	No. of eggs	51	102	318	
	Larvae and pupae %	300	44	129	158
1935	No. of eggs	57	>61	117	
	Larvae and pupae %	496	205	238	313
1936	No. of eggs	145	25	>94	
	Larvae and pupae %	62	168	509	246

It will be seen that not only is there no correspondence between the abundance of eggs and larvae pupae in any one generation but that there is no regularity in the discrepancies. It can only be concluded that for an insect such as *P. rapae* small concentrated plots do not provide a good method for estimating the abundance. I believe that the only satisfactory method would be to have 20 or 30 small plots (say four plants each) scattered over a large area (several square miles). This would allow for local concentrations of the butterfly, while the replication of the plots would allow of some determination to be made of the accuracy of the estimations. Such a method would, however, be extremely laborious in practice. For the purpose of studying insect numbers (where it did not matter what species was studied), it would be better to take a species whose food plant grew in large continuous areas.

C. FACTORS AFFECTING POPULATION DENSITY

8. General considerations

An insect which, like *P. rapae*, lays 300–400 eggs must have about 99% of each generation killed off if the species is not to increase. Moreover, with that high egg number, a decrease of 1% in the death-rate means that the species will start the next generation with the population three times as dense. It is impossible, working on a small scale, to obtain anything like the accuracy required to show whether, in any particular generation, the death-rate has been 98 or 99%. Actually, there is a considerable mortality which has not been investigated in detail at all. Thus the deaths amongst the pupae have not been studied because that stage is almost impossible to find under natural conditions (except in the first generation, where many larvae pupate on the cabbage plants).

Of the factors which affect density, some are very much easier to study quantitatively than others. The percentage parasitism is easily obtained with fair accuracy. Deaths due to diseases (virus, etc.), to predators and to climate

are almost impossible to estimate accurately without more elaborate technique than is at present available. The data for sterility and parasitism of eggs and for the deaths due to predators, to micro-organismal diseases and to climate will first be briefly considered. Later the much more extensive data for deaths due to insect parasites will be discussed.

9. Sterility and parasitism of the eggs

During the routine examination of the plots in 1933–36, a certain number of eggs was observed to shrivel up without any sign that they had been attacked by predators. Out of 1337 eggs, 17 (1·3%) certainly failed to hatch. Some of these may have been attacked by mites but, on the other hand, some may have failed to hatch which were merely recorded as disappearing from their ring on the leaf, so that the figure of 1·3% may be about correct. Under cage conditions, a considerably higher proportion of the eggs is sometimes sterile, but this is very likely due to the conditions under which they have been laid. Of the 1337 eggs, 303 (23·6%) were actually seen to hatch (see below) but probably nearly all did so.

On the Continent, an egg parasite, *Trichogramma evanescens* Westw., has been bred from *Pieris rapae* (Faure, 1926; Voukassovitch, 1926, etc.). No egg parasites of any Pierine have been observed at Slough. Of *P. rapae* 112 wild-laid eggs have been reared at different times, and 303 eggs from the routine examinations were seen to hatch in the open, that is, a first-stage larva was found within 1 cm. of a marked egg on the first examination at which an egg was found to be absent from its ring on the leaf. Moreover, no eggs have been noticed to go black in the way those do which have been attacked by *Trichogramma*.

10. Predators

The following references to predators of *Pieris* spp. have been found in the literature: (1) eggs: *Reduviolus lativentris* (Boh.) (Hemiptera, Nabididae) (Anon. 1917); (2) larvae: *Reduviolus ferus* (L.) (Faure, 1926), *Polistes gallicus* (L.) (Vespidae) (Faure), *Vespula germanica* (Fab.) (Faure; Twinn, 1924), *Xanthandrus comptus* (Harr.) (Syrphidae) (Faure), birds; (3) pupae: *Polistes gallicus* (L.), *Vespula germanica* (Fab.); (4) adult: *Libellula* spp. (Odonata) (Faure, 1926), birds.

No observations have been made on the action of birds, though it is likely that they are at least moderately important enemies of the pupae. Occasionally, on fences near the Slough Field Station, pupae have been found which seem to have been eaten by birds, but no estimate of the importance of this check can be made.

Other predators noticed include: mites, spiders, bugs (Anthocoridae, Nabididae), lacewings (*Chrysopa carnea* Steph.), ladybirds (Coccinellidae) and Syrphid flies.

The mite was a large red one, *Allothrombium fuliginosum* (Hermann)

(kindly determined by Mrs A. M. Hughes). It was found chiefly on wild crucifers or on dense beds of seedling cabbages, where the conditions are more like a weedy patch than a plot. The mites were seen to eat *Pieris* eggs and in captivity one ate seven eggs in three days.

A large number of spiders (kindly identified by Dr A. R. Jackson) has been found on cabbage, but they appear mainly to eat flies, aphides and parasitic Hymenoptera. A young female of *Theridion pallens* Bl. was however seen to eat a first-stage *Pieris* larva on 16 August 1933.

Of bugs, the most important are species of *Anthocoris*, especially *A. nemoralis* (Fab.). The nymphs have been more often seen than the adults and, like the mites, they are much more often found on wild crucifers than on cabbage plots. On such plants as *Sisymbrium officinale* quite a high proportion of the eggs are eaten by these bugs and many collapsed egg-shells are found. In captivity, a nymph ate seven out of eight eggs during one night and on the next day it ate one egg and one second-stage larva. I believe these bugs have a considerable importance as checks on the *Pieris* living on wild crucifers but very rarely attack those living on cultivated cabbages. Two species of *Reduvio*lus, *R. ferus* (L.) and *R. flavomarginatus* (Scholtz), have been seen on cabbage but have not been observed to eat *Pieris* larvae at Slough.

None of the other insect predators has been seen to eat *Pieris* larvae though they probably do occasionally. The *Chrysopa* larva eats mainly aphides, but was once seen eating a Syrphid larva. Coccinellid larvae (chiefly *Coccinella bipunctata* L. and *Adonia variegata* (Goeze)) are not uncommon but probably eat aphides as a rule. The Syrphids are also chiefly aphid eaters, but the larva of *Sphaerophoria scripta* (L.) was once seen to eat a young larva of the moth *Mesographe forficalis* (L.).

To sum up: invertebrate predators are quite unimportant checks except on wild crucifers. Birds are certainly of some importance, especially as enemies of the pupa, but their effect has not been closely estimated (cf. p. 260).

In 1935, a special study was made of the combined effect of all causes of prepupal death other than parasites. Over the period 12 May–16 July eight cabbages a day were uprooted from a series of plots. The cabbages to be uprooted were chosen at random, the arrangement being fixed before the start of the experiment. Each cabbage was carefully pulled to pieces and the eggs and larvae on it recorded. Table 13 gives the result of the examination.

The second to eighth columns give the number of each stage found on successive dates on the 56 cabbages which were examined each week. The ninth column gives the weekly totals. The last column gives the numbers which would be expected from the routine egg counts described on p. 255. These have been adjusted to allow for the different number of cabbages being examined. The discrepancies between the figures in columns nine and ten are chiefly due to the extreme irregularity of the oviposition of *Pieris*; but the smaller numbers actually found in the weeks ending 23 June and 30 June than

would have been expected from the oviposition record are probably due to some larvae leaving the cabbages for pupation (compare also p. 256 and Table 11).

Table 13

Week ending (1935)	Eggs	Larval instars I	II	III	IV	V	Pupa	Totals	Nos. derived from weekly egg counts	Difference
19 May	12	0	0	0	0	0	0	12	19	− 7
26 May	20	0	0	0	0	0	0	20	25	− 5
2 June	14	11	1	0	0	0	0	26	31	− 5
9 June	16	10	6	0	1	0	0	33	37	− 4
16 June	17	8	11	2	2	0	0	40	40	0
23 June	5	3	4	6	5	3	0	26	43	−17
30 June	1	1	2	5	6	5	1	21	43	−22
7 July	0	0	3	1	2	13	3	22	—	—
14 July	0	0	0	0	2	1	7	10	—	—
15–16 July	(5)	0	0	0	0	1	2	3	—	—
Totals	85*	33	27	14	18	23	13	213	—	—
Expected proportions	28·6	21·4	14·3	15·7	19·5	37·2	76·2	213	—	—
Proportions expected with 85 eggs	85	64	43	47	58	113	232	642	—	—
Duration of stages	6	4·5	3	3·3	4·1	7·8	16	44·7	—	—

* Omitting the five eggs of the second generation found on 15–16 July.

Row eleven in the table gives the total of each stage found during the period. In general, the numbers of each stage found should correspond to the time spent in that stage. Data as to the duration of each stage at 15·7° C. have been taken from Table 4 and form row fourteen of Table 12. These data are not strictly applicable over a range of temperatures (the mean temperature for 12 May–16 July was 14° C.) but they serve as a guide for the present discussion. Row twelve of the table shows the total of 213 eggs, larvae and pupae divided up into numbers proportional to the duration of each stage. The number of eggs actually found was far more, and of fifth-stage larvae and pupae far less than would have been expected. This is probably chiefly due to larvae leaving the cabbages to pupate and only slightly due to the death of larvae though probably the larger larvae are more liable to attack by birds. The effect of the migration of mature larvae can be eliminated by calculating the numbers of each stage which might have been expected in a random collection containing 85 eggs. These numbers are shown in row thirteen of the table. The discrepancy between the numbers of first-, second-, third- and fourth-stage larvae in rows eleven and thirteen gives a measure of the mortality. Instead of the 212 which would have been expected, only 92 were discovered. Probably, therefore, about half these younger larvae are destroyed either by predators or by rain, wind, etc.

I believe that in suitable conditions and on a larger scale this method might give valuable indications of larval mortality. The essential condition (not easy

to obtain in an enclosed area) is a homogeneous area of the food plant so large that the removal of substantial samples for examination makes no difference to the attractiveness of the area for oviposition.

11. Parasites other than insects

Under natural conditions, deaths due to protozoal, fungal or virus diseases have been so rare during the period of the present work that they have not been studied. One or two larvae dead of a mould-like fungus were seen at Wicken Fen, Cambridgeshire, in August 1934. Apparently, a similar disease (*Entomophora sphaerosperma* Fres.) sometimes destroys large numbers of *P. brassicae* in Germany (Friederichs, 1931). Moss (1933) suggests that 60% of the caterpillars are killed by "disease". This estimate, however, was based on the number of deaths observed in captivity. All Pierine larvae are highly susceptible to "wilt" when kept indoors whether crowded in large cages or kept singly in small tins. The number of these deaths probably has no proportionate relationship to the number of those occurring out-of-doors from the same causes.

The following data for the mortality of larvae and pupae in captivity were obtained from all not parasitized by other insects; this includes besides larvae used in experiments, a few small collections made in Kent, Hampshire and Cambridgeshire. The data are analysed first according to the stage in which the insect was brought into the laboratory, secondly according to the year and generation. The figures in Table 14 suggest that the larvae have "wilt" in a dormant condition which is brought out by being kept in captivity. On the whole, the longer they are kept in captivity (i.e. the earlier the instar when they are brought in), the more likely they are to die. Eggs, however, produce more viable larvae, perhaps because they are less likely to be infected. Table 15 (p. 262) shows that there is a general tendency for the mortality to increase from the first to the third generation, the mean percentage mortality being 31·6, 46·2 and 58·3% respectively. It is very doubtful, however, if these figures indicated the extent of the mortality in nature.

Table 14

		Larval instars						
	Egg	I	II	III	IV	V	Pupa	Totals
Total bred	62	221	248	346	512	788	153	2330
% dead as larva	21	57	40	36	31	13	—	26·8
% dead as pupa	6	15	17	25	27	28	22	23·9
% emerged	72	28	43	39	42	59	78	49·3

12. Climate

No special investigations were made of the effect of climate on the multiplication of *P. rapae*. A drop in temperature during an oviposition period

usually results in a fall in the number of eggs laid. This was particularly well shown in the May frost of 1935:

	May			
1935 May–June week ending	13	20	27	June 3
Mean weekly temperature	11·1° C.	5·0° C.	11·1° C.	12·2° C.
No. of eggs laid	17	11	2	16

Dull and cloudy weather also seem to reduce the activity of the adults. Occasionally, young caterpillars have been found half drowned in the water collected in cabbage leaves after rain. What mortality is due to this and similar factors is unknown; data bearing on this question have already been given in Table 13.

Table 15

Year	1932		1933		1934			1935			1936			
Generation	I	III	I	III	I	II	III	I	II	III	I	II	III	Totals
Total bred	97	133	164	288	17	425	251	220	50	292	82	38	275	2330
% dead as larva	5·1	6·8	4·3	12·8	0	13·2	42·6	46·4	74	45·5	43·9	18·4	32·4	26·8
% dead as pupa	9·3	28·6	23·2	53·1	6·0	23·1	29·1	4·1	2·0	18·8	15·9	7·9	21·9	23·9
% emerged	85·6	64·6	72·5	34·1	94·0	63·7	28·3	49·5	24·0	35·7	40·2	73·7	45·8	49·3

A more general picture of the relation between climate and abundance of *P. rapae* is given in Table 16. This shows the relation of numbers of larvae and pupae collected in the various generations to mean temperature and mean weekly rainfall during the period of that generation. 1936 has been omitted as rainfall records are not available (see note, p. 286) and one figure (107) is rather uncertain since the collecting methods were still unstandardized during generation I, 1932.

Table 16. *Relation of abundance of larvae and pupae to mean temperature and mean weekly rainfall in various generations*, 1932–35

Year	Generation	Mean weekly rainfall in mm.	Mean temperature during relevant period, °C.	No. of larvae and pupae collected
1935	III	20·50	13·28	278
1935	I	20·00	14·50	283
1934	III	12·00	13·66	411
1932	III	11·00	13·55	364
1933	I	10·75	16·44	526
1934	II	10·25	16·39	451
1933	III	7·50	15·55	379
1932	I	6·75	16·83	(107)
1935	II	1·50	17·61	121
1934	I	0·00	14·89	153

As far as these figures go, they suggest that *P. rapae* is more abundant when both rainfall and temperature have intermediate values. This can be expressed numerically by saying that *P. rapae* exceeds its mean abundance when the product of the deviations of temperature and rainfall (measured as above) from their mean values lies between −3·179 and +0·602; or, ignoring

signs, when this product does not exceed 3·18. On the two occasions when the number of larvae and pupae collected was greatest (526, 451), the products of these deviations were least (+0·602, +0·176).

13. Insect parasites

The check exercised by insect parasites is the easiest of the controlling agencies to investigate. The chief disturbing factor is the considerable local variation in the parasite rate, i.e. differences between plots quite close to one another in the Field Station grounds. Just as in estimating the abundance of *Pieris*, it would be better to average a number of small samples over a wider area.

On p. 258 it has already been shown that there are apparently no egg parasites at Slough, so that larval and pupal parasites only are dealt with. The following parasites of larvae have been bred at Slough: Braconidae, (*a*) *Apanteles rubecula* (Hal.), (*b*) *A. glomeratus* (L.); Tachinidae, (*c*) *Phryxe vulgaris* (Fall.), (*d*) *P. nemea* (Mg.), (*e*) *Phryxe* sp., (*f*) *Epicampocera succincta* (Mg.), (*g*) *Compsilura concinnata* (Mg.).

No secondary parasites have been bred from the Tachinids, though their puparia may be attacked by them in the soil. The following parasites have been bred from the *Apanteles*: Chalcididae, *Tetrastichus rapo* (Walk.); Ichneumonidae, *Mesochorus tachypus* Hlgr., *Astomaspis nanus* (Grav.) (*Hemiteles fulvipes* Grav.), *A. submarginatus* (Bridgm.) (not from *A. glomeratus* at Slough) and *H. areator* (Pz.) (not from *A. rubecula* at Slough).

The only pupal parasite bred has been (*h*) *Pteromalus puparum* (L.) (Chalcididae). In sections (*i*) and (*j*) the interrelations of the parasites and the parasitic interrelations of the hosts are considered respectively.

A very much larger number of both primary and secondary parasites has been recorded in the literature; most of them are discussed by Faure (1926) but some additional ones have been recorded by Russian and American workers. The most remarkable absentee amongst the parasites is the Ichneumonid, *Anilastus ebeninus* (Grav.), recorded as a rather common parasite of both *P. rapae* and *P. brassicae* on the Continent. In England, a species which Mr J. F. Perkins tells me he cannot distinguish from the Continental *Pieris* parasite has been bred from *Gonepteryx rhamni* (L.). It is difficult to understand why this parasite of the brimstone butterfly does not attack species of *Pieris* in England; but my own quite extensive records and the much larger collections of Moss (1933) seem to show that it does not, at any rate in the South. It is just possible that certain Hymenopterous eggs and larvae found in dissected caterpillars of *P. rapae* in 1932 but not seen in other years may belong to this parasite. In August–September 1932, 9 second-stage, 71 third-stage, 70 fourth-stage and 141 fifth-stage larvae of *P. rapae* were dissected. Unknown parasites were found in six third-stage larvae (three parasitic

larvae, one also with *A. glomeratus*, and three eggs) and in two fourth-stage larvae (one egg and one with three larvae). The eggs were small, oval, brown bodies and the larvae had long tails like Ichneumonids of the group Campoplegini. In one host an empty egg-shell was found with the larva. No such larvae or eggs have been seen since 1932 and no adult parasite which could correspond to them has been bred.

In breeding larvae to determine the percentage parasitism certain precautions have been taken. All larvae and pupae which died were dissected to see if they contained parasitic larvae; hosts dying in the first instar are too small to search thoroughly for parasites, so they have been excluded. Larvae from which parasites emerged have also been dissected to see if they contained other parasitic larvae. It is necessary to record the instar of each larva, since the younger instars have not been exposed to the chance of parasitism so long as the older ones, and this will affect the apparent percentage parasitism. All the parasites dealt with invariably kill the host.

(*a*) *Apanteles rubecula* (Hal.)

This is a parasite almost specific to *P. rapae*. It does not appear to attack *P. napi* (of which 33 larvae have been bred at different times). Very exceptionally it will attack *P. brassicae*. Of 1181 larvae of that species reared five have produced *A. rubecula*. Hamilton (1935-36) failed to obtain ovipositions in either *P. napi* or *P. brassicae* in captivity. The same writer found that, as in most *Apanteles*, it was mainly the first instar of *P. rapae* which was attacked. The following records of all the bred and dissected larvae provide data on this point; all *A. rubecula* are enumerated, including those that were attacked by secondary parasites.

Table 17. *Attack by* A. rubecula *on different host instars*

Larval instar	No. collected	No. parasitized by *A. rubecula*	%
I	243	63	25·9
II	293	87	29·7
III	524	169	32·3
IV	1126	448	39·8
V	1240	59	4·8
Totals	3426	826	24·1

If the attacks were entirely restricted to the first instar the parasite rate would be the same in all instars after the first. The small difference between the percentage parasitism in instars I, II and III shows that most oviposition occurs early in the first instar, though there may be a little ($<3\%$) at the beginning of the second. The apparent rise in the percentage parasitism of the fourth instar is certainly due to the difficulty of determining the instar of parasitized larvae. When the parasite larva is large, the host larva becomes stunted and a fifth instar is easily mistaken for a fourth. At least 9–10% of the so-called parasitized fourth instar must really have been fifth. The parasite

bites its way out of the host at the end of the fourth or in the fifth instar, so that the apparent parasite rate is reduced when mature larvae are collected. When desiring to compare the parasite rate on two areas it is better to omit fifth instar larvae unless their number is nearly the same in the two collections.

Altogether 1116 *A. rubecula* from all sources have been bred at Slough during 1932–36. This number is made up as follows:

Table 18. *Breeding records of* A. rubecula

	Totals	♂	♀
Larvae found in dissected hosts	50	—	—
Larvae found in hosts which died	81	—	—
Cocoon formed: parasite larva died	143	—	—
parasite pupa died	11	—	—
parasitized	123	—	—
adult died in cocoon	43	24	19
adult emerged	647	302	345
sex undetermined	6	—	—
cocoon lost	12	—	—
Totals	1116	326	364

This works out at a sex ratio of 0·9 males : 1·0 females.

Apanteles rubecula is intrinsically superior to all other parasites of *P. rapae* mentioned in the present paper. It is almost invariably a solitary parasite. It is probable that the females are capable of recognizing host larvae which already contain eggs or larvae of the same species. If the females lack this power, then additional eggs or larvae must die at a very early stage, for they have not been found when host larvae have been dissected. One larva only (fifth stage *P. rapae*, 3 September 1935) was found to contain two quite large larvae of *A. rubecula* together with a second-stage larva of *Phryxe vulgaris*.

Hibernation takes place as a resting larva inside the cocoon. Just as in *P. rapae*, a gradually increasing number of the parasites fail to emerge in the autumn and enter a diapause. If the cocoons are kept indoors, a rather greater number emerge, but even under these conditions most of them hibernate. The hibernating cocoons when kept indoors have a rather high mortality, mostly in the larval stage, just before pupating; this may be due to lack of moisture which could be remedied. Once they have entered the diapause, warm conditions do not make them emerge much earlier. One or two adults emerged in January–February, but most in March, April and especially May. If the cocoons are hibernated out of doors (in an unheated shed), the adults emerge in May and June. Certain pupae begin to enter diapause about 20 August and from then onwards an increasing proportion hibernate, as shown in Table 19. Occasionally an individual will skip a generation, e.g. a hibernating pupa emerge in July instead of May–June.

Table 20 shows the dates on which individuals emerged during 1932-36, the summer being divided into fortnightly periods. There are clearly at least four generations a year and there may well be more in some families. The great length of the oviposition of *P. rapae* in generations 3–4 makes first-stage larvae available for a long period.

Table 19. *Hibernation of* A. rubecula *pupae*, 1932–36

Date cocoon was formed	Emergent ♂	Emergent ♀	Dormant ♂	Dormant ♀	% Dormant
15–31 August	26	30	6	3	13·8
1–15 September	40	46	19	27	34·8
16–30 September	23	18	47	33	66·1
1–22 October	7	12	25	35	76·0

Table 20. *Dates of emergence of* A. rubecula, 1932–36

	Before May	May		June		July		August		September		October	After 15 October
Date		1–15	16–30	1–15	16–30	1–15	16–31	1–15	16–31	1–15	16–30	1–15	
No. emerging	12	18	102	66	29	60	41	101	110	51	126	30	10
Generation	I (hibernated pupae)					II		III				IV	

A small experiment was carried out to determine the duration of the early stages of *A. rubecula* at controlled temperatures. First-stage larvae of *P. rapae* were offered to *A. rubecula* females in glass tubes; after stinging (and presumably oviposition) had been observed, the larvae were transferred to incubators. Some of the stung larvae proved to be unparasitized and no host larvae survived at 32 and 12° C., but the following results were obtained:

Table 21. *Life history of* A. rubecula *in days*

Temperature (°C.)	No. of larvae	Duration of egg + larval period	Duration of pupal period	Total pre-adult period	Preadult period of *P. rapae*
17	5	15–18 (16·6)	8–11 (9·4)	26·00	37·20
22	5	10–11 (10·4)	5–6 (5·75)	16·15	26·45
27	6	7–9 (7·8)	4–5 (4·75)	12·55	21·80

The figures in brackets are means.

Thus at all three temperatures *A. rubecula* develops more rapidly than its host, but proportionately more so at 27° C. than at 17° C.

In the literature, there are a number of statements to the effect that larvae (more particularly of *P. brassicae*) living on plants other than cabbage (especially *Tropaeolum* and *Capparis*) are very little attacked by parasites. This appears to be substantially true at Slough of *P. brassicae* on *Tropaeolum*. In August September 1936 many larvae were found both on cabbage and *Tropaeolum* and the following parasite rates were obtained:

Table 22. *Parasitism of* P. brassicae *on cabbage and* Tropaeolum

Stage	Cabbage II	Cabbage III	Cabbage IV	Cabbage V	*Tropaeolum* II	*Tropaeolum* III	*Tropaeolum* IV	*Tropaeolum* V
No. of larvae collected	2	28	62	102	69	49	28	104
Unparasitized	0	0	10	70	69	49	28	104
A. glomeratus	2	27	51	32	0	0	0	0
A. rubecula	0	0	1	0	0	0	0	0
Phryxe vulgaris	0	1	0	0	0	0	0	0
% parasitism	58·8				0			

From other localities, I have some records of parasitized larvae of *P. brassicae* on *Tropaeolum*, but the rate is usually low.

Very much less extensive data are available for *P. rapae* living on plants other than cabbage. Moreover, in many cases the scattered individuals of such plants as *Sisymbrium alliaria* and *S. officinale* grow very near to cabbage patches. At any rate, as far as the data go they do not show that caterpillars living on weeds or scattered plants are less parasitized. The following are the combined records for larvae obtained from *Sisymbrium alliaria*, *S. officinale*, horse-radish, turnip, mustard, *Tropaeolum* and *Cardamine hirsuta*. The average parasitism by *A. rubecula* on these plants was 26%.

Table 23. *Parasitism of* P. rapae *on plants other than cabbage*

Stage	I	II	III	IV	V
Total collected	14	17	14	20	8
Unparasitized	10	15	8	6	8
A. rubecula	3	1	3	12	0
A. glomeratus	1	1	2	1	0
Tachinids	0	0	1	1	0

In spite of this result, there is a very considerable difference in the parasite rate in different areas on the Field Station grounds. In the first place, a distinction can be made between cabbages grown in open fields with the plants well spaced out ("field conditions") and those grown in sheltered corners with the plants usually closer together ("garden conditions"). The data for the years 1934–36 are analysed in this way in Table 24.

Table 24. *Comparison of parasitism of* P. rapae *by* A. rubecula *under field and garden conditions (fifth instar larvae omitted)*

		No. with	
Field conditions:			
Instar	No. collected	*A. rubecula*	
I	86	9	
II	87	7	
III	201	49	
IV	483	155	
Totals	857	220	25·7% parasitism
Garden conditions:			
I	118	45	
II	118	63	
III	105	62	
IV	237	174	
Totals	578	344	59·5% parasitism

It is evident that caterpillars on plants in sheltered situations where the cabbages are often grown closer together are more than twice as heavily parasitized. It is difficult to dissociate this effect from that of host density, for the number of larvae per cabbage is always greater in garden conditions and it will be shown later (p. 270) that the percentage parasitism is also higher when the host density is greater.

Further evidence on this point has been obtained by experiments on larvae

placed on cabbages in pots. The pots were placed in a variety of situations and the density of *Pieris* larvae was always high. Where, therefore, parasitism was low it can be asserted that this was because the situation was unfavourable, not because the host density was low. The experiments were carried out over the years 1933-36 and the methods used were approximately the same. Between 5 and 25 first-stage larvae were placed on small cabbage plants in pots; the pots stood on selected sites for 7-18 days, the larvae being brought in when in the second or third instar. Sometimes as many as half the larvae had disappeared by the end of the experiment, partly because they had been eaten by Anthocorids or washed off by rain but also because they wandered off the plant, which was probably often too small to support so many larvae.

The results of the experiments were extremely uniform and it is unnecessary to describe them in great detail. Effects of host-density, of varying number of parasites available, and of different exposure periods were completely obliterated by the effect of site. Larvae on pots exposed amongst grass or in flower beds were never parasitized by *A. rubecula* whereas the control larvae on pots exposed amongst cabbage plots were heavily parasitized. This did not apply to the polyphagous Tachinid parasites (see p. 280). A summary of the results is shown in Table 25.

Table 25. *Parasitism by* A. rubecula *of* P. rapae *larvae in different habitats*

Place	No. of pots	No. of larvae	Distance from nearest cabbage plots m.	% parasitism by *A. rubecula*
Cabbage plots	7	193	0	50
On lawn	8	63	28	0
On herbaceous border	9	101	65	0
In field	4	13	46	0

This table strongly suggests that the parasites are attracted in the first place to large areas of cabbage and then proceed to hunt for larvae. The smallest area of plots contained a hundred plants. The lawn is an open site, but the herbaceous border is well sheltered. A few experiments were made to find out how far *A. rubecula* would wander from a cabbage plot. In none of them was the parasitism reduced compared with that on the plot. The following trials were made:

Table 26. *Parasitism by* A. rubecula *at different distances from cabbage plots*

Distance from plot m.	Nature of site	No. of larvae	No. parasitized by *A. rubecula*
18	By horse-radish (over hedge)	5	3
9	Amongst potatoes	7	5
2–11	Six pots spaced out amongst wheat stubble	21	11
2–11	Six pots spaced out amongst parsnips	32	20
3	Amongst parsnips	12	10

The extent of parasitism by *A. rubecula* partly depends on the density of the larvae of *P. rapae*. On the average, the more larvae there are per cabbage, the higher the rate of parasitism. In the years 1933–36 there were nine different areas of cabbage grown. Collections were made during the three generations of most years, making altogether 35 lots available for study. The number of plants in an area varied from 37 to 864 and the number of larvae in a collection varied from 10 to 215. The densities (i.e. number of caterpillars per cabbage) ranged from 0·023 to 1·022, with a mean of 0·248. The parasitism (expressed as parasites per host larva) varied between 0·00 and 1·00, with a mean of 0·3014. The correlation between density of *Pieris* larvae and number of *A. rubecula* for the 35 collections works out at +·5109, which is significant ($P < 0{\cdot}01$). This implies that the parasites show a tendency to congregate in the areas where the host is most numerous. This may have a buffer effect on the population, hindering both complete extinction and too rapid multiplication of the host.

This effect is complicated by the tendency of *A. rubecula* to prefer "garden" to "field" conditions already noted (p. 267). On the whole, the areas where the densities of *Pieris* larvae and of *A. rubecula* are high are those with "garden" conditions, as shown in the following table:

Table 27. *Effect of "field" and "garden" conditions on host density*

Range of density	Examples in "garden"	Examples in "field"
0·683–1·022	2	2
0·411–0·486	2	1
0·306–0·371	3	1
0·229–0·296	4	1
0·104–0·149	2	6
0·23 –0·97	0	11

Since the expressions "field" and "garden" conditions cannot be expressed quantitatively, it is not possible to separate this effect from that of density. In fact if the correlations between density and parasitism for field and garden conditions are worked separately, they come to +0·4135 and +0·2693 respectively. Neither of these correlations is significant, but this may be in part because fewer records are available. It should be noted that no allowance has been made for variations in the average parasitism in different years or generations; such variations would tend to obscure the simple density effect.

One observation has been omitted from the above discussion since the density was quite unusually high. This was made on a small group of six cabbages growing under garden conditions in September 1934; the six plants produced 65 larvae (density 10·8, parasitism 0·78), one plant alone having 17 larvae. This was by far the highest density observed under completely natural conditions, though sometimes a single plant in a covered frame which has temporarily been left open may be very heavily infested.

It might be expected that when hosts were present above a certain density, parasitism would fall since there would be insufficient parasites to lay in every host. Some attempts were made to investigate this in field experiments. They met the almost insuperable difficulty that larvae tend to wander off plants on which they are crowded. Table 29, however, gives the results obtained in 1934. Similar experiments in 1936 were a failure since too few larvae were left at the end of the experiment. First-stage larvae were exposed for one week on potted plants amongst cabbages growing in the garden. The number attacked by *A. rubecula* is expressed as a fraction of the final number of hosts.

Table 28. *Experiments on effect of host density on parasitism by* A. rubecula, *August* 1934

No. of pots	No. of larvae per plant		Total no. of larvae		No. attacked by *A. rubecula*	
	Range	Mean	Initial	Final	Total	Fraction
6	2–10	6·0	35	18	16	0·9
3	15–25	21·0	64	27	24	0·9
5	40–80	65·0	325	203	150	0·74

It is just possible that at the very high density of about 65 larvae per plant, a protective effect is beginning to be apparent; it is certain from this experiment, from the unsuccessful experiments in 1936 (when there was no evident difference in parasitism for one, four or eight larvae per plant) and from field collections, that the density at which a protective effect is observed is well above ten larvae per plant, at least when the parasites are as abundant as they were at Slough, 1932–36.

The parasites of *A. rubecula* have already been listed on p. 263 and they will now be considered in more detail. The most important is *Tetrastichus rapo* (Walk.) which attacks *A. rubecula* inside the *Pieris* larva; the complete data (including some collections made outside the Field Station grounds) for the years 1932–36 is given in Table 29. Only hosts which might have been expected to produce parasites are included; *A. rubecula* larvae which were obtained by dissection or specimens which died as larvae in the cocoon are omitted, since the *Apantèles* larvae were not themselves dissected. Cocoons which produced *Mesochorus* are omitted since it is not known which parasite is intrinsically superior. Evidently the bulk of the oviposition takes place in fourth-stage host larvae. The apparent drop in the parasitism of fifth-stage host larvae is almost certainly due to chance, the number of this stage collected being too low. The absence of any significant difference between the percentage parasitism of fourth-stage host larvae and of *Apanteles* cocoons is of some interest because it proves that *T. rapo* (Walk.) never attacks the cocoon of its host. Picard (1922) observed a strain scarcely separable (cf. Ferrière & Faure, 1925) from *T. rapo* (Walk.) which attacked the cocoons of *Apanteles*. No later worker has recovered this strain and it certainly does not seem to occur in England.

T. rapo lays its eggs through the body wall of the host and inside the

Apanteles larva. On one occasion several fifth-stage larvae of *P. brassicae* were found which were covered with females of *T. rapo*. Later these larvae produced large numbers of *Apanteles glomeratus* cocoons which themselves produced a number of *T. rapo*. Apparently *T. rapo* occasionally fails to place its eggs inside the *Apanteles* larva; several times loose larvae (almost certainly those of *T. rapo*) have been found in the body cavity along with an *A. rubecula* larva. Usually such loose larvae are associated with curious masses of tissue which is perhaps the sign of phagocytic action.

Table 29. *Percentage parasitism of* A. rubecula *by* T. rapo *according to the stage in which the primary host* (P. rapae) *was collected*

	Host stage					*Apanteles*
	I	II	III	IV	V	cocoons
No. collected	114	146	161	289	31	115
No. with *Tetrastichus*	0	2	7	45	3	20
% with *Tetrastichus*	0	1·4	4·4	15·6	9·7	17·0

The number of *T. rapo* bred from a single host varied between 1 and 20 (usually 3–12, average 7·3), but it was found during the later stages of the work that a number of *Tetrastichus* larvae and pupae either died in the cocoon or emerged long after the first batch. Thus many of the records are too low. There is usually an excess of females; altogether 183 males and 401 females being reared; about a quarter of the broods are unisexual. The hibernation of *T. rapo* (Walk.) follows a very similar course to that of *A. rubecula*.

Mesochorus tachypus Hlgr. is an Ichneumonid with habits similar to *Tetrastichus rapo* and, like that species, lays its eggs within the larvae of *Apanteles rubecula* and *A. glomeratus* while these are still in the host. *M. tachypus* Hlgr. has commonly been referred to in Continental literature of *M. angustatus* Thoms., while Moss (1933) used the name *M. pectoralis* Ratz. (which is probably not really a synonym). Mr J. F. Perkins, who established the above synonymy for me, also states that *M. gracilis* Brischke is probably also a synonym. *M. tachypus* oviposits in a wide variety of hosts; at Slough it has been bred from the following (besides *P. rapae* and *P. brassicae*): *Plutella maculipennis* Zett. (*Angitia fenestralis* (Hlgr.) or *A. cerophaga* (Gr.)), *Lycaena phlaeas* (L.) (*Apanteles* sp.), *Mesographe forficalis* (L.) (*Apanteles gabrielis* Gaut. and Riel). Mr Perkins also has records of a number of other hosts. The incidence of attack on *A. rubecula* during 1932–36 is given in Table 30. Cocoons which produced *Tetrastichus rapo* have not been counted since it is not known which of these secondary parasites is intrinsically superior. Probably because of the rarity of the parasite, the figures are not high enough to show any regularity in the attacks on different host stages. On the average about 4% of the *A. rubecula* are destroyed by this parasite.

The species of *Astomaspis* and *Hemiteles* attack the cocoons of *Apanteles* and have therefore no direct relation to *Pieris*. *Hemiteles areator* (Pz.) has not

been bred from *A. rubecula* at Slough though it has been recorded to attack it on the Continent. *A. nanus* (Grav.) (*Hemiteles fulvipes* Grav. of most authors) and *A. submarginatus* (Bridgm.) are both uncommon parasites at Slough. Of the 100 cocoons not producing either *T. rapo* or *Mesochorus*, two produced males of *A. nanus* and three *A. submarginatus* (1♀, 2♂). As the cocoons by being brought into the laboratory escaped some of their normal exposure to these parasites, it is probable that they destroy rather more than 5% of *A. rubecula* cocoons.

Table 30. *Parasitism of* Apanteles rubecula *by* Mesochorus tachypus

	Host stage					*Apanteles* cocoons
	I	II	III	IV	V	
No. collected	116	150	157	260	29	98
No. with *Mesochorus*	2	6	3	16	1	3
% with *Mesochorus*	1·7	4·0	1·9	6·2	3·4	3

(*b*) *Apanteles glomeratus* (L.)

A. glomeratus is essentially a parasite of *P. brassicae* and only secondarily attacks *P. rapae*. There are records of attack on a large number of other Lepidoptera, but it is certain that these records are nearly all due to misidentifications.

Just as in *A. rubecula*, oviposition is almost restricted to host larvae in the first two instars. Unlike *A. rubecula*, the larvae of the parasite are gregarious, any number between two and over a hundred being found inside a single host. The higher numbers are certainly due to successive ovipositions, probably by different females. The larvae leave the host at a later stage than those of *A. rubecula*, normally just after the host larva has spun itself down and is about to pupate. After the larvae have emerged and started to spin, it will often be found, on dissecting the dying host larva, that a certain number of *Apanteles larvae* have been left behind, as shown by Hamilton (1935). The actual figures of this loss of larvae (Table 31) show that it is not usually very important.

Table 31. *No. of larvae of* A. glomeratus *failing to leave host*

No. of larvae		0	1	2	3	4	5	6	7	8	9	10	11	12	14	15	17	20
Frequency:	*P. brassicae*	62	31	11	3	7	5	1	2	1	1	2	0	2	1	1	1	1
	P. rapae	9	7	3	1	1	0	0	0	0	1							
	Totals	71	38	14	4	8	5	1	2	1	2	2	0	2	1	1	1	1

The wastage of larvae in this way works out at 4·7% for *P. rapae* as host and 4·9% for *P. brassicae* as host; this compares with the figure of 2·8% obtained by Hamilton for both species combined. Apparently as many as 20 can be left behind and yet those which have emerged appear to be healthy and mostly to reach the adult stage. Sometimes the larvae left behind have been of two sizes, suggesting that such larvae may have been derived in part from

a second oviposition. In a few cases, much higher numbers (16+, 21+, 50, 62, 67), larvae were left inside the host, but in these examples those larvae which did emerge either failed to spin or at any rate all failed to reach the adult stage. Death from this cause tends to occur when the total number of parasitic larvae is higher than usual. In one case, it was clearly associated with very severe hyperparasitism by *Tetrastichus rapo* (Walk.). A group of 13 fourth- and fifth-stage larvae of *P. brassicae* was found, 15 June 1933, in which every larva had three or four adults of *Tetrastichus* sitting on it. Every caterpillar contained *A. glomeratus* larvae, most of which died (Table 32).

Table 32. *Heavily parasitized larvae of* P. brassicae

No. of host larvae	No. parasitized by *A. glomeratus*	No. of hosts died before *A. glomeratus* emerged	No. of parasite groups died without spinning	No. of *A. glomeratus* broods producing *Tetrastichus*
13	13	5	4	4

In other examples, failure of *Apanteles* larvae to leave the host and also failure to spin if they have left appear to be due to a "wilt" disease, possibly directly contracted from the host. The total effects of this cause of death were as follows: *P. brassicae*, 297 larvae contained *A. glomeratus*, eight of these larvae (2·7%) died before the parasites emerged, six (2·0%) broods of parasites died before spinning; *P. rapae*, 24 larvae contained *A. glomeratus*, one died before the parasites emerged.

When the *A. glomeratus* spin their cocoons, even in successful broods, there are sometimes one or two larvae which die without spinning. I have no numerical estimate of this cause of death, but I should be surprised if it accounts for more than 2% of the larvae. Within the cocoon, the parasite may die as a larva or as a pupa or the adult may fail to bite its way out. It is difficult to estimate the importance of this mortality in the field; it results in a large number of deaths in the laboratory, perhaps being due in part to insufficient moisture. The highest mortality occurs in hibernating larvae, of which only a small proportion produced adults. It will be seen from Table 33 that three-quarters of the larvae spinning cocoons in June–July emerged. In August–October 54% emerged and of these nearly all came out in the same year, only 180 (2%) adults emerging in the spring. Possibly if the cocoons had been placed out of doors as soon as they were formed the mortality would have been less. Putting them out of doors from the middle of October onwards produced no marked improvement.

There appear to be two somewhat prolonged periods of emergence during the summer, not counting the hibernated individuals which emerge in May–June. It is also possible that there is at least a partial third emergence in the autumn. The data are presented in Table 34. The individuals emerging between 1 October and 31 May are from cocoons which had been kept indoors; those emerging between 1 June and 30 June are from cocoons hibernated out of doors.

Probably much fewer would emerge in October if all the cocoons were put out of doors as soon as they were formed, but I believe there would still be a considerable emergence in the late autumn.

Table 33. *No. of adults emerging from cocoons of* A. glomeratus

Host	Host generation	No. groups of cocoons	No. of cocoons	No. of adults emerged	% emergence	Sex ratio
P. brassicae	I	26	1155	880	76	0·81♂ : 1♀
	II	245	7756	4165	54	0·82♂ : 1♀
P. rapae	I	20	587	425	72	0·37♂ : 1♀
	III	16	322	199	62	0·42♂ : 1♀
Totals	—	307	9820	5669	58	0·75♂ : 1♀

Table 34. *Emergence of adult* A. glomeratus

Host	January 1 to April 30	May 1–15	May 16–31	June 1–15	June 16–30	July 1–15	July 16–31	August 1–15	August 16–31	September 1–15	September 16–30	October	October 16 to December 31
P. brassicae	180	4	1	59	9	812	0	0	27	541	1676	1425	297
P. rapae	0	0	0	0	238	187	0	0	19	88	78	0	0
Totals	180	4	1	59	247	999	0	0	46	629	1754	1425	297

First-stage larvae of *P. brassicae* are available during 1–15 June and in August. The first brood must, therefore, be attacked by hibernated adults; the second by the survivors of the July emergence. Most of the *Apanteles* which emerge in September must fail to find *P. brassicae* larvae, since a third brood of this species is quite exceptional. First stage *P. rapae* larvae are available throughout the autumn, but, as is shown later (p. 275), *A. glomeratus* does not attack this species very much under natural conditions. The result is, therefore, that *A. glomeratus* does not have its life cycle well-attuned to that of its principal host under English climatic conditions. In south and central France, where *P. brassicae* appears to have three generations regularly, the relation of host to parasite must be much better adjusted.

The only records of the number of eggs laid by *A. glomeratus* are those of Hamilton (1935: 265) obtained at Slough. The number of observations is unfortunately small, but the rarity of *A. glomeratus* at Slough after the first two years of the present work made it impossible to repeat his experiments. His figures for four larvae of *P. rapae* were 15, 25, 25, 27 (average 23) and for 15 larvae of *P. brassicae* 2 to 54 (average 30·5). These counts were made on caterpillars which had been stung once in the laboratory. The number of *A. glomeratus* obtained from caterpillars collected in the field is shown in Table 35. This includes all the records except those made in 1932 when no

Table 35. *No. of* A. glomeratus *larvae per host*

Host	Number of larvae 1–5	6–10	11–15	16–20	21–25	26–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100	101–110	111–120	121–130
P. rapae	4	3	7	13	10	11	8	12	4	1	0	0	0	0	0	0
P. brassicae	1	9	14	41	67	42	74	63	21	7	9	6	4	1	1	2

allowance was made for *A. glomeratus* larvae left behind in the host after the majority had pupated. The higher numbers in Table 35 are certainly partly due to multiple oviposition but it is impossible accurately to estimate how much. Probably for *P. rapae* larvae the average number of eggs in one oviposition is about 18, so that 36, 54 and 72 larvae, respectively, correspond *on the average* to two, three and four ovipositions in a single host. Similarly in *P. brassicae*, the average number of eggs in one oviposition is *on the average* 25, and 50, 75, 100 and 125 larvae correspond to two, three, four and five ovipositions, respectively. Owing to the great variation in the actual number of eggs laid in a single oviposition, it is not possible to say how many multiple ovipositions there were. The average number of parasites per host in *P. rapae* is 27·6 and in *P. brassicae* 38·4. The higher figure in *P. brassicae* is certainly partly due to the greater amount of multiple oviposition in its larvae. If, however, only caterpillars which had fewer than 26 parasites in them are considered, the average number of parasites in such caterpillars in *P. rapae* is 16 and in *P. brassicae* 19 so that the parasite clearly has some power of regulating egg-number in relation to the host.

The figures for the average parasitism of *P. rapae* and *P. brassicae* during 1932–36 are given in Table 36, based only on larvae collected at Slough. No allowance has been made for the instar in which the larvae were collected as this would not make much difference to the results.

Table 36. *Parasitism of* Pieris *by* A. glomeratus *at Slough*

		P. rapae		*P. brassicae*	
Year	Generation	No. of larvae collected	% parasitism	No. of larvae collected	% parasitism
1932	I	100	1	0	—
	II	0	—	328	88·7
	III	363	11·6	—	—
1933	I	434	16·7	29	86·2
	II	0	—	7	100
	III	372	1·0	—	—
1934	I	143	0	0	—
	II	444	0·5	0	—
	III	408	0	—	—
1935	I	263	0	17	29
	II	119	0	12	58
	III	277	0	—	—
1936	I	89	0	0	—
	II	40	0	523	29·6
	III	476	0	—	—
Totals		3528	3·4	916	53·5

Most previous workers (e.g. Picard, Faure, Moss) have noted that *P. brassicae* is always more heavily parasitized than *P. rapae* by *A. glomeratus*. Most writers have suggested that this difference is due solely to the difference in the habits of the two hosts—*P. brassicae* being gregarious (not solitary) and living more exposed on the surface of the leaves. The second difference is much less

important than it seems at first sight. The larger larvae of *P. rapae* mostly hide in hearts of cabbages, while the larvae of *P. brassicae* at all stages feed on the outer leaves, usually on the underside. Nevertheless, at the time when *A. glomeratus* lays its eggs (instars I and II) the larvae of *P. rapae* are also on the outer leaves, since the whole of the first instar and often much of the second is spent on the outer leaves where the egg was laid.

Significance of the gregarious habit of *P. brassicae* in relation to parasitism is a complex question. Supposing that the two species of larvae are present in equal numbers on an area, *P. rapae* will be widespread in rather small numbers over most of the area, while *P. brassicae* will be present in a small number of groups, each consisting of about 10–70 larvae. Without very much more elaborate experiments than have yet been made, it is impossible to say whether it is easier for a parasite to discover a number of scattered larvae or the same number of larvae concentrated into a few widely separated groups. In field studies, it is necessary to distinguish between the number of groups parasitized and the percentage parasitism in each group. The need for this was not at first realized, so that only scanty data are available. Altogether, of 19 groups 13 (68%) were parasitized; with the available data, there was no evidence that the size of the group affected either its chance of being parasitized or the amount of parasitism within it. It is probable, however, that with larger collections some sort of density effect would be found, as in *A. rubecula*. The only conclusion that seems justified at the moment is that *A. glomeratus*, as already suggested by Gautier (1919), normally attacks *P. rapae* only when *P. brassicae* is present. This seems to be clearly shown by the comparison of the parasitism of the two species in Table 36 and also by the failure of *A. glomeratus* to establish itself in New Zealand (*P. brassicae* being absent) where it was introduced to control *P. rapae* (private communication by Mr J. Muggeridge).

When considering the parasitism within the host group, the degree to which a female can distinguish parasitized from unparasitized larvae is of the greatest importance. If the female lacks much power of discrimination, a high rate of parasitism will only be attainable at the expense of much multiple oviposition. The unknown in the problem is the number of separate acts of oviposition which gave rise to the 53·5% parasitism of 916 larvae of *P. brassicae*. On the hypothesis of random oviposition, it can be shown from the formula given by Salt (1932), that if the number of separate ovipositions was x, then

$$916\left(1-\frac{1}{916}\right)^{x}=426,$$

$$x=701.^{1}$$

From this figure it can be calculated, again on the hypothesis of random oviposition, that there would be 326, 125, 32 and 6 cases of larvae oviposited

[1] 426 = number of unparasitized larvae. In part of these calculations it is necessary to use at least seven-figure logarithm tables.

in one, two, three and four times respectively. Taking 25 eggs as the average number laid at each oviposition, this works out at 17,400 parasites produced by 490 caterpillars, an average of 35·5 per caterpillar. This agrees pretty closely with the number actually observed, 38·4, and would suggest that there is little discrimination. Unfortunately, so many hypotheses are involved that little certainty can be felt as to this result.

The secondary parasites which attack *A. glomeratus* have much less importance than those which attack *A. rubecula*, since usually only a few of the larvae in any one group of parasites are killed. The data for attack by *Mesochorus tachypus* Hlgr. and *Tetrastichus rapo* (Walk.) are given in Table 37.

Table 37. *Parasitism of* A. glomeratus *by* Mesochorus *and* Tetrastichus

	Cocoons		Groups attacked by		Actual numbers bred			
Primary host	groups	individuals	*Mesochorus*	*Tetrastichus*	*Mesochorus*		*Tetrastichus*	
P. rapae	36	947	1	5	6♂		24♂	38♀
P. brassicae	231	7713	9	14	9♂	12♀	172♂	212♀

This shows that in *P. rapae* about 2 % and 14 % of the groups were attacked by *Mesochorus* and *Tetrastichus*. But (allowing six *Tetrastichus* per cocoon) of the total number of cocoons, only 0·6 and 1 % of the individual parasites were destroyed by these parasites. The figures for *P. brassicae* are 3·9, 6·3 % and 0·3, 0·8 %.

Besides these parasites which attack the *Apanteles* when still within its host, a very large number of parasites of the cocoons have been bred on the Continent (see Faure, 1926). At Slough, only two of these *Astomaspis nanus* (Grav.) (*Hemiteles fulvipes* Grav.) and *Hemiteles areator* (Pz.) have been bred in small numbers. Actually only a very few groups of *A. glomeratus* cocoons were found in nature, perhaps largely because most of the *P. brassicae* larvae on the area were collected. It is unlikely that the control exercised by these secondary parasites at Slough was more than 1 % of the total number of cocoons.

A. glomeratus is intrinsically inferior when in competition with *A. rubecula*, which leaves its host at an earlier stage; but these two parasites were very rarely found in the same host (see p. 283). *A. glomeratus* is superior to the Tachinids which do not leave their host till its pupal stage.

(*c*) *Phryxe vulgaris* (Fall.)

This is the commonest of the Tachinid parasites of *Pieris*, though even so the percentage attack is usually low. This is probably partly because it is extremely polyphagous and there are a great many other hosts available. The species of *Phryxe* are not at all easy to distinguish and after the field side of the present work had been completed, Mr C. J. Wainwright discovered that there were one or two more unrecognized British species. These seem to be rare

and it is probable that the great majority of specimens recorded as *P. vulgaris* really were that species. A small amount of confusion, especially in the larval stage, is almost inevitable. The female lays an egg on the skin of the host and the larva soon hatches and burrows in. On one occasion a fourth-stage larva of *P. rapae* was seen to turn round and bite off an egg which had been laid upon it in captivity. The larva forms a connexion with one of the host tracheae and lives invested in a sheath. The structure of the larval instars has been figured by Bisset (1938).

The host stages attacked by *Phryxe vulgaris* are shown in Table 38. It will be seen that nearly all oviposition occurs in the fourth and fifth host stages. The best estimate of the average parasitism over the five-year period is obtained by considering only stages IV and V and the pupa of *P. rapae*. If these stages alone are considered, the parasitism is 8·6%.

Table 38. *Stages of* P. rapae *attacked by* P. vulgaris *at Slough*

Host stage	No. collected	No. parasitized	%
I	243	0	0
II	293	1	0·3
III	524	14	2·7
IV	1126	95	8·4
V	1240	106	8·5
Pupa	155	17	11·0
Totals	3581	233	6·5

Phryxe vulgaris is an extremely polyphagous parasite and attacks representatives of many families of Lepidoptera. At Slough, besides *P. rapae*, it has been bred from *P. brassicae* (949 larvae collected, 16 containing *Phryxe*, average parasitism 1·7%), *Mesographe forficalis* (L.), *Plusia gamma* (L.) and *Pararge megaera* (L.).

Table 39. *Mortality table of early stages of* Phryxe vulgaris *in captivity*

	1 larva per host	2 larvae per host	3 larvae per host	4 larvae per host
No. emerged as adults	115	10	1 (1♂ 2♀)	—
Host died	36	3	2	1
Host with *Apanteles rubecula*	63	6	3	—
Host with *A. glomeratus*	3	—	—	—
Phryxe died in puparium	11	—	—	—
Totals	228	19	6	1
Host dissected before death	29	3	2	—
Totals	257	22	8	1

Table 39 gives the survival and mortality of all *Phryxe vulgaris* (including some from sources other than Slough, but all from *P. rapae*) bred in captivity and also the number of occasions that one, two, three or four *Phryxe* larvae have been found in a single host. Three adults were the most ever successfully emerging from a single host pupa, but four larvae were once found in a host

which died. The sex ratio of those which emerged was 0·9 males : 1 female (67 males, 71 females). *P. vulgaris*, like all the Tachinids, is intrinsically inferior to all the Hymenopterous parasites (including *Pteromalus puparum* (L.)); there are no data as to the results of competition amongst the different species of Tachinids.

If the data for Slough alone are considered it is possible to examine how far the amount of superparasitism by *Phryxe* agrees with the hypothesis of random oviposition of single larvae at a time. The observed figures are compared in Table 40 with those calculated from the formula given by Salt (1932). The relatively small departure from the calculated values might be explained by assuming that sometimes two or three larvae are laid at one oviposition instead of always one.

Table 40. *Superparasitism by* P. vulgaris *at Slough*

	Observed	Calculated
Total number of fourth- and fifth-stage and pupae	2510	—
No. not parasitized by *Phryxe*	2292	2269
No. with 1 *Phryxe*	192	230
No. with 2 *Phryxe*	17	11
No. with 3 *Phryxe*	8	<1
No. with 4 *Phryxe*	1	<1

On the available evidence, *P. vulgaris* shows no tendency to be attracted to the areas where *P. rapae* is densest. An examination of 25 separate collections, estimating the density and the amount of parasitism from stages four and five and pupae of the host, showed no relation between density and amount of parasitism.

There is some information as to the correlation between parasite and host instars. This was obtained from dissecting *P. rapae* larvae and pupae; the data are summarized in Table 41.

Table 41. *Correlation of* Phryxe *and* Pieris *instars*

Host stage ...	III	IV	V	Pupa
Nos. of *Phryxe*, instar I	4	22	25[1]	0
II	0	1	25	2
III	0	0	2	7

In all the specimens I have studied, the winter has been passed as a larva (certainly third stage) inside the host pupa. If kept indoors, the larva emerges for pupation in December–February; if kept out of doors, in April–May. As the summer proceeds an increasing number of larvae enter diapause, i.e. fail to leave the host pupa. Thus all parasites (20) from hosts collected in July emerged the same year; from hosts collected in August, 44 emerged the same year and 21 hibernated, these being mainly from hosts collected towards the end of the month; in September hosts, two *Phryxe* emerged the same year and 17 hibernated.

[1] This includes two lots of three and one of four; possibly the rate of development of the parasites is slowed up when they are crowded.

There appear to be at least three generations a year as shown in Table 42, where the limits of the generations are shown. The three peaks of emergence corresponding fairly closely with the three periods when young larvae of *P. rapae* are most abundant.

Table 42. *Emergence of adult* Phryxe (*all sources*)

December–March	April	May 1–15	May 16–31	June 1–15	June 16–30	July 1–15	July 16–31	August 1–15	August 16–31	September 1–15	September 16–30	October 1–15	October 16–November
4♂ 2♀*	5♂ 4♀*	1♂	12♂ 6♀	1♂ 9♀	0	1♂ 3♀	13♂ 14♀	2♂ 1♀	10♀ 14♀	9♂ 12♀	6♂ 3♀	2♂	0
		I				II		III					

* All but two of these individuals were hibernated indoors. The exceptional individuals (1 ♂, 1 ♀) emerged in March although hibernated out of doors.

The total duration of the life history is not known but there are records of the period between host pupation and the emergence of the *Phryxe* larva and of the pupal period, under uncontrolled laboratory conditions. These are given in Table 43, the two periods being dealt with according to the month in which they were passed. The first-named period corresponds pretty closely with the third instar of the *Phryxe* larva. It will be seen that in general the female develops a little more slowly than the male. The third instar lasts for 1–8, usually 4 or 5 days, and the pupal period is 11–20, usually 12–16 days. The total pre-adult period appears to be about the same as that of *Pieris*, but a much greater proportion of it is spent as a mature larva or pupa.

Table 43 *Duration of third instar and pupal period in* Phryxe

	June		July		August		September	
Month	♂	♀	♂	♀	♂	♀	♂	♀
Duration third instar (days)	3	5–7 (6)	3–6 (4·4)	1–7 (4·6)	4–8 (5·8)	4–8 (5·7)	5–8 (6·25)	—
Duration pupal period (days)	13	—	11–15 (11·4)	12–15 (13·2)	13–17 (14·5)	14–20 (15·2)	13–18 (15·7)	14–18 (16·5)
No of individuals	1	3	9	13	13	15	9	13

The figures in brackets are the means.

In consonance with its polyphagous habits, *Phryxe vulgaris* shows no evident attraction to areas of cabbage. In one small experiment 61 young larvae of *P. rapae* were exposed on a potted plant in a cabbage plot and 56 larvae were exposed over the same period on other pots in the herbaceous border. Both lots produced three *Phryxe* larvae. *Phryxe* also appears to prefer sheltered, "garden" conditions to more open "field" conditions. Considering only fourth- and fifth-stage larvae and pupae of the host, 302 hosts showed 17·5% parasitism under garden conditions, while 1111 hosts showed 8·9% parasitism under field conditions.

As already stated, no secondary parasites of *P. vulgaris* have been bred, but these would mainly be expected from pupae formed out of doors and these have not been found.

(*d*) *Phryxe nemea* (Mg.)

This is another polyphagous species extremely similar both in its structure and biology to *P. vulgaris*. It appears to have a somewhat different range of hosts and is much less common as a parasite of *P. rapae*. The following are the records of its occurrence:

Pieris pupa collected 12 July 1932, puparium 15 July, ♂ emerged 29 July 1932.

Fifth-stage larva 14 August 1934, pupa 20 August, puparium 22 September, ♀ emerged 1–21 March 1935.

At Slough it has also been bred from a Geometrid on hawthorn. The structure of the puparium has been illustrated by Bisset (1938).

(*e*) *Phryxe* sp.

During the last two years, Mr C. J. Wainwright has been studying the British species of *Phryxe* and has found that there is at least one unrecognized species which has been confused with *P. vulgaris*. One specimen of this peculiar form was bred from *P. rapae* at Slough:

Fifth-stage larva 28 September 1933, pupa 30 September, puparium 2–6 March 1934, ♀ emerged 19–23 March 1934.

The normal hosts of this form seem to be species of *Zygaena* and *Z. lonicerae* (Esp.) and *Z. trifolii* (Esp.) occur at Slough, abundantly in some years. Mr W. H. Goddard bred a large number of this *Phryxe* from *Z. lonicerae* at Slough in 1936.

(*f*) *Epicampocera succincta* (Mg.)

This is another Tachinid with habits similar to *Phryxe* though apparently less polyphagous and perhaps more definitely attached to Pierine hosts. I have bred it from *P. rapae* at Slough, Buckinghamshire, Goudhurst, Kent and Wicken Fen, Cambridgeshire; Mr A. H. Hamm bred it from the same host at Oxford. Baer (1921) mentions *Saturnia pavonia* (L.) as a host. The early stages have been described by Bisset (1938).

The relation between the stage of the host and the percentage attack is shown in Table 44. The number bred is clearly too small to be sure which stage is attacked most but it looks as if younger larvae were more attacked than in *Phryxe*. This is supported by certain experiments (see p. 282). The puparium seems to be less hardy than that of *Phryxe* and of 22 puparia obtained (all

Table 44. *Stages of* P. rapae *attacked by* E. succincta *at Slough*

Host stage	No. collected	No. parasitized	%
I	243	0	0
II	293	1	0·3
III	524	3	0·6
IV	1126	4	0·4
V	1240	3	0·2
Pupa	155	2	1·3
Totals	3581	13	0·4

sources), eight failed to produce adults; the 14 which gave adults produced 5 males and 9 females. Hibernation appears to take place as a third-stage larva within the host pupa (one record). Twelve of my specimens emerged in September, two in August and one (hibernated) in May. It is probable that there are really three generations a year, as in *Phryxe*. The time elapsing between the formation of host pupa and the emergence of the parasite larva was 2–5 (average 4) days and the duration of the pupal stage 11–15 (average 13) days, under laboratory conditions. In July 1935, a number of young larvae of *P. rapae* were exposed in and near one of the sheltered cabbage patches ("garden" conditions). After a week's exposure, 93 second- and third-stage larvae were brought in and these produced 11 *Epicampocera* (one host containing two first-stage larvae, the only example of more than one larva per host noted in this species). Similarly, young larvae were exposed on potted cabbages on the herbaceous border 5–12 June 1934 and 21–8 August 1933. In 1933, 27 second-stage larvae brought in produced eight *Epicampocera*; in 1934 39 second-stage larvae produced three *Phryxe* and six *Epicampocera*. These rates of parasitism are very much higher than have been observed in any of the routine collections. It appears likely that *Epicampocera*, even more than *Phryxe*, prefers sheltered situations such as those in which the pots were exposed. It is possible the relatively high density of the larvae on the plants also attracted the flies. The experiments also seem to show that *Epicampocear* attacks young larvae more freely than does *Phryxe*.

(*g*) *Compsilura concinnata* (Mg.)

This is another extremely polyphagous parasite which lays its eggs in the gut of the host by means of a curved spike at the end of the female abdomen. At Slough, besides *Pieris brassicae* and *P. rapae*, it has been bred from *Smerinthus ocellatus* (L.), *Porthesia chrysorrhoea* (L.) (=*similis* Fuessl.) (commonly), *Acronycta aceris* (L.) (commonly), *Mamestra brassicae* (L.), *M. pisi* (L.), unknown Noctuid and *Hyponomeuta padella* (L.). It appears to attack *P. brassicae* (949 larvae collected, 15 containing *Compsilura*, average parasitism 1·6%) rather more commonly than *P. rapae* (3581 larvae and pupae collected, four containing *Compsilura*, average parasitism 0·1%). It would appear from the data on both species of *Pieris* combined that larvae from the third to fifth stage are attacked and that up to two may be found in one host. There would appear to be three generations a year and hibernation seems to take place the same way as in *Phryxe*. The early stages have been described by Culver (1919) and Bisset (1938).

(*h*) *Pteromalus puparum* (L.)

This is a well-known Chalcid parasite of many butterfly pupae. Much information on its biology is contained in the paper by Faure (1926). It has always been rare at Slough as a parasite of *P. rapae*, even allowing for the

relatively small number of pupae collected. I suspect that pupae collected from palings, etc., rather than from cabbages would show a much higher parasite-rate. Of 155 pupae collected, six produced *Pteromalus*, average parasitism 3·9%. The true rate, for pupae which had been exposed to attack for the full period, would be somewhat higher, perhaps 6%.

(*i*) *Interrelations between different species of parasite*

Which parasite is successful when in competition with one of the others has already been noted, but the numerical data as to the effects of this competition are given below.

It has been recorded (p. 277) that the two species of *Apanteles* almost never come into competition, apparently owing to the discrimination exercised by ovipositing females; moreover, probably for the same reason, two larvae of *A. rubecula* are hardly ever found together (p. 235). Repeated oviposition in one host certainly occurs in *A. glomeratus* (p. 275) but, owing to the special habits of this species, there has to be a very high degree of superparasitism for this to have an injurious effect (p. 274). In places where it is common, *Pteromalus puparum* can exercise a considerable check on the Tachinids but it was too rare at Slough to obtain any information on this point.

The only serious competition at Slough, therefore, was between *A. rubecula* (and to a much less extent *A. glomeratus*) and the Tachinids. Only one case of competition between different species of Tachinid was noted, a fourth-stage larva, 18 September 1934, contained *A. rubecula* (later producing *Tetrastichus*) and one first-stage larva of both *Epicampocera* and *Compsilura*. In Table 45, the numerical data as to competition are set out.

Table 45. *Competition between Tachinids and* Apanteles *based on* 3426 *larvae and* 144 *pupae of* P. rapae *collected at Slough*

Parasite species	Hosts with only this parasite	Hosts with parasite + *A. rubecula*	Hosts with parasite + *A. glomeratus*
Phryxe vulgaris	158	66	9
Phryxe vulgaris (fourth-stage hosts only)	43	50	2
Epicampocera	7	5*	1
Compsilura	2	2*	0

* These two numbers include the single larva which contained both *Epicampocera* and *Compsilura*.

In the above table only larvae obtained in routine collections are included, not those which were exposed in experiments. Hosts which contained two or more of a parasite have been counted as one record only. It will be seen that 32% of *Phryxe* and about half of the individuals of the other two Tachinids are indirectly destroyed by the *Apanteles*. The question at once arises whether this destruction is due purely to the chance oviposition of two species in one host or whether they show some mutual attraction or repulsion. It is best to consider this question amongst the fourth-stage larvae only since younger

ones have hardly been exposed to the attack of *Phryxe* and in older ones most of the *A. rubecula* have already left for pupation. All individuals containing *A. glomeratus* have been omitted from the calculation. There are then 1110 host larvae; 93 contained *Phryxe* and 448 contained *A. rubecula*. The expected number of larvae containing both parasites on the hypothesis of random association is $\frac{93 \times 448}{1110}$ or 37·5. This does not differ significantly from the observed number, 50 (P between 0·1 and 0·05).

(*j*) *Interrelations of the hosts and their parasites*

The most important parasite of *P. rapae*, *A. rubecula*, is practically confined to it. It has been shown, however, that *A. glomeratus*, which may be of some importance in certain years, is chiefly attracted to *P. brassicae* so that the presence or absence of this host may have a considerable effect on *P. rapae* (p. 275). No alternative hosts of *Epicampocera* are known at Slough. *Phryxe vulgaris* and the much less important *P. nemea* are so polyphagous that probably no one host has any great influence on their movements and abundance. Of the 13 species of Lepidoptera which have been found feeding on cabbage, *P. vulgaris* has been found to attack only *P. rapae*, *P. brassicae*, *Plusia gamma* and *Mesographe forficalis*. It has already been noted (p. 281) that the undescribed species of *Phryxe* probably attacked *P. rapae* because of the presence of its main host, *Zygaena*, in the neighbourhood. *Compsilura*, although very polyphagous, seems to have some preference for hairy larvae, and it attacks *P. brassicae* more commonly than *P. rapae*. It has also been bred in small numbers from the cabbage Noctuid, *Mamestra brassicae*. It seems to be much more common as a parasite of *Acronycta aceris* (on horse chestnut) and *Porthesia chrysorrhoea* (on hawthorn, etc.). There are no data to discuss the host relationships of *Pteromalus puparum* at Slough.

The secondary parasites also seem to be either rather specific parasites or else very polyphagous. *Tetrastichus*[1] and the two species of *Astomaspis* seem to attack only the *Apanteles* living on *Pieris*. *Hemiteles areator* and *Mesochorus* seem to be polyphagous.

The numbers of primary parasites obtained are given in Table 46. These figures are expressed as percentages in Table 47, only effective parasitism being shown (i.e. *A. rubecula* + Tachinid is counted only as *A. rubecula*). The data for mean temperature and mean weekly rainfall during the periods when the collections were made is also included. An examination shows that there is no significant correlation between the amount of parasitism and temperature and humidity measured in this way. In *A. rubecula*, there is a general tendency each year for the parasitism to increase with each generation. In *Phryxe vulgaris*, the most parasitism seems to occur in the second generation.

[1] *T. rapo* has been bred from *Anilastus ebeninus* (Grav.) in *Pieris* on the Continent.

Table 46. *Summary of parasitism of* P. rapae *at Slough*, 1932–36

Year	Generation	Hosts collected: Larvae	Hosts collected: Pupae	*A. rubecula*: Alone	*A. rubecula*: + *Phryxe*	*A. rubecula*: + *Epicampocera*	*A. rubecula*: + *Compsilura*	*A. rubecula*: + *Epicampocera* + *Compsilura*	*A. rubecula*: + *A. glomeratus*	*A. glomeratus*: Alone	*A. glomeratus*: + *Phryxe*	*A. glomeratus*: + *Epicampocera*	*Phryxe vulgaris*	*Epicampocera*	*Compsilura*	*Phryxe nemea*	*Phryxe* sp.	*Pteromalus*	Unknown Hymenopterous larva
1932	I	100	7	3	0	0	0	0	0	1	0	0	6	0	0	1	0	0	0
	III	363	1	16	4	0	0	0	0	36	6	0	18	3	0	0	0	0	7
1933	I	434	92	54	0	0	0	0	0	66	3	0	3	2	0	0	0	2	0
	III	372	7	103	14	2	0	0	2	3	0	1	24	1	0	0	1	0	0
1934	I	143	10	31	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
	II	444	7	136	10	0	1	0	0	2	0	0	32	0	2	0	0	0	0
	III	408	3	137	23	2	0	1	0	0	0	0	26	0	0	1	0	0	0
1935	I	263	20	37	3	0	0	0	0	0	0	0	22	1	0	0	0	2	0
	II	119	2	45	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0
	III	277	1	108	11	0	0	0	0	0	0	0	1	0	0	0	0	1	0
1936	I	89	1	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	II	40	2	15	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	III	476	2	57	1	0	0	0	0	0	0	0	15	0	0	0	0	0	0
Totals*		3528	155	755	66	4	1	1	2	108	9	1	158	7	2	2	1	6	7

* So far as these totals differ from those given in other tables, it is due to the inclusion of larvae whose instar was not determined.

Table 48 shows the yearly incidence of the parasites of *A. rubecula*—*Tetrastichus rapo* and *Mesochorus tachypus*. Only wild specimens from Slough which might have produced parasites (i.e. not dissected specimens) are included. The numbers differ from those in Tables 29 and 30 in omitting parasites obtained from caterpillars exposed in experiments.

Table 47. *Effective percentage parasitism of chief parasites of* P. rapae *at Slough*, 1932–36

Year	Generation	Hosts collected (larvae and pupae)	*A. rubecula* %	*A. glomeratus* %	*Phryxe vulgaris* %	Mean temperature °C.	Mean weekly rainfall in mm.
1932	I	(107)	3	1	6	16·83	6·75
	III	364	10	12	7	13·55	11·00
1933	I	526	29	15	1	16·44	10·75
	III	379	48	1	8	15·55	7·50
1934	I	153	18	0	1	14·89	0·00
	II	451	46	0·3	15	16·39	10·25
	III	411	56	0	2·4	13·66	12·00
1935	I	283	28	0	12·6	14·50	20·00
	II	121	49	0	17	17·61	1·50
	III	278	61	0	0·8	13·28	20·50
1936	I	90	32	0	0	15·00	?*
	II	42	44	0	4	14·89	?
	III	478	24	0	3	13·72	?

* Owing to the death of Mr A. E. Williams who kept the rainfall records, the records for 1936 have been lost.

Table 48. *Parasites of* A. rubecula *larva bred at Slough*, 1932–36

Year	Generation	No. of hosts bred	No. producing *T. rapo*	*M. tachypus*
1932	I	5	0	0
	III	12	3	1
1933	I	84	11	0
	III	104	21	2
1934	I	12	0	0
	II	131	8	7
	III	181	18	6
1935	I	34	0	2
	II	26	2	1
	III	121	7	2
1936	I	8	0	0
	II	9	0	0
	III	53	0	1
	Totals	780	70	22

14. Conclusions

An attempt may now be made to see how far the causes of death enumerated account for the failure of the species to multiply unduly. If we started with the average egg number of 350 (p. 248) the history of these may be followed. If the species is not to increase 348 of the eggs must on the average be killed off. Present information can only account for 264 of these. I suspect that nearly

all the rest are destroyed by birds and other predacious enemies of the last larval instar and pupa, but it has not yet been found possible to evaluate this cause of mortality under natural conditions.

Table 49. *Causes of mortality in* Pieris rapae *at Slough*

	No. of eggs left	Cause of death	% reduction	No. of *Pieris* destroyed
I	350	Sterility, predators, disease, climate, before stage V	50 (p. 260)	175
II	175	*A. rubecula*	40 (p. 264)	70
III	105	*A. glomeratus*	3·5 (p. 275)	4
IV	101	Tachinidae	10·5 (p. 285)	10
V	91	*Pteromalus*	6·0 (p. 283)	5
VI	86	Predators of stage V and pupa	?97·7	?84

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E. SUMMARY

1. All stages of the three British species of *Pieris* are distinguished.

2. The life history of the small white, *P. rapae* (L.), is described; in particular the food plants, the oviposition site, the lengths of the stages at different temperatures, the place of pupation, the sex ratio, the number of generations a year, and the factors determining hibernation are discussed.

3. The study of the fluctuations of the numbers of *P. rapae* was based on egg counts and on collections of larvae and pupae. The limitations of these methods are discussed.

4. The effects of climate on *P. rapae* are briefly dealt with; it seems to be favoured by mean temperatures between 15·55 and 16·66° C., associated with a mean weekly rainfall of 7·5–12·5 mm.

5. A few unimportant insect predators are noted; birds, which are possibly important predators, were not directly studied.

6. Non-insect parasites (? viruses) cause many deaths in the laboratory but probably a very much smaller mortality, which is difficult to estimate, in nature.

7. The following insect parasites were encountered: Braconidae, *Apanteles rubecula* (Hal.), *A. glomeratus* (L.); Tachinidae, *Phryxe vulgaris* (Fall.), *P. nemea* (Mg.), *P.* sp., *Epicampocera succincta* (Mg.) and *Compsilura concinnata* (Mg.); Chalcididae, *Pteromalus puparum* (L.). The first three were the only important ones and their biology is described in some detail; especially the relation of

A. rubecula to host density and of *A. glomeratus* to the presence of *Pieris brassicae* (L.), its main host.

8. The following secondary parasites of the two species of *Apanteles* were bred: Chalcididae, *Tetrastichus rapo* (Wlk.); Ichneumonidae, *Mesochorus tachypus* Hlgr., *Astomaspis nanus* (Grav.) (=*Hemiteles fulvipes* (Grav.), *A. submarginatus* (Bridgm.) and *Hemiteles areator* (Pz.). The first two are the most important and their biology is dealt with in some detail.

9. Summarizing the causes of mortality, it is found that the factors studied in the present paper would account for 264, or 75%, of the 350 eggs laid by an average female. The remaining 84, which must be destroyed if the species is not to increase, are probably eaten by birds and other predatory enemies of the pupal and fifth larval instars.

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THE INTERTIDAL ZONE OF TWO STREAMS AND THE OCCURRENCE OF *GAMMARUS* SPP. ON SOUTH RONA AND RAASAY (INNER HEBRIDES)

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(*With* 1 *Figure in the Text*)

1. Introduction

The distribution of animals in a region of transition between two environments is of obvious interest. The junction of fresh with sea water conditions has been studied mainly in estuaries, where the organisms are either free-swimming, floating, or mud burrowers. Owing to tidal movements and the variation of salinity with depth it is difficult to determine the range of conditions to which the first two are subjected and the burrowers are able to find regions where they are independent of the salinity fluctuations of the overlying water (Reid, 1930, 1932; Alexander *et al.* 1932). At the mouth of a rapidly flowing stream, however, it is usual to find the substratum of the intertidal zone overlain by pebbles or large stones under which a relatively stationary population of animals is living, subjected to environmental changes resulting from the tidal movements. The distribution of these animals can be determined fairly accurately and correlated with the tidal levels. Pantin (1931) made a survey of this kind on a stream at Wembury mainly with the object of determining the range of conditions experienced by the flatworm *Procerodes* (*Gunda*) *ulvae*; and Pyefinch (1937) has investigated the mouth of a stream on Bardsey Island.

Apart from tidal movements, other factors which may influence the distribution of animals in this type of environment include: (*a*) the volume and the physical and chemical condition of the stream water; (*b*) the gradient of the stream bed, which will determine the rate of flow; (*c*) the composition of the stream bed, i.e. the size of the stones and sand particles on which the stones lie; (*d*) discontinuous factors such as rain storms. Both (*b*) and (*c*) will determine the rapidity with which the salinity of the water under the stones will follow the salinity fluctuations in the water above (Reid, 1932). Ideally, if the effects of the various factors are to be properly determined, such a survey should be made several times in the year and on a number of streams.

During a fortnight's stay on the island of South Rona (Inner Hebrides) in July 1937 we were able to make a survey of two streams. Whilst we fully realize the limited value of two single sets of observations, it is of interest to

compare them with the results of Pantin. A close comparison with the work of Pyefinch is not possible, since the intertidal zone of the Bardsey Island stream was of a different type (a series of rock pools) and the gradient of the stream bed was not determined.

The fresh waters of South Rona comprise two small lochs (Loch Braig and a small unnamed one), several isolated and probably temporary pools and a number of streams. The streams, of which six were examined, are small and flow rapidly over rocky ground to the seashore. All the fresh waters investigated were neutral (*p*H 7·0–8·0).

2. Surveys of streams II[1] (dry harbour) and IV[1] (big harbour)

These two were selected because they were conveniently placed and were discharging approximately the same amount of water. Since the zones included between the spring and neap tide levels differed considerably in slope it was hoped that a comparison might be of interest.

The level of fixed points above datum was determined by means of a clinometer and tape measure. As a base-line for all measurements the high-tide level on a calm day was taken to be the height above datum recorded for Stornoway in the *Admiralty Tide Tables*. This is admittedly an assumption, but the method probably established a reasonable correspondence between the fixed points in the two streams surveyed. Sections of these are shown in Fig. 1, and above each are figures denoting the proportion of the total number of high tides which would theoretically cover a given point. They are calculated from the tide tables for Stornoway during July and August 1937, and of course take no account of the effect of winds. The extent to which a storm could raise the high-tide level was shown by the accumulation of a line of dead weed on the grass well above the highest tide level (Fig. 1, Stream II).

Collections of animals were made at various points in the stream bed in order to determine the limits of each species. The extent of the grass and seaweeds is also shown in Fig. 1, though the former did not actually occur in the stream bed but on either side at a higher level. It was therefore not inundated to the extent indicated in the figure.

The bed of II was fairly uniform. From *A* to *C*, where it was about 2 ft. wide, it consisted of small stones resting on coarse gravel with occasional larger stones. At *C* there was a rather sudden drop of about 2 ft. over large boulders. From *C* to *H* the bed was similar to that between *A* and *C*. Below *H*, which was well below the lowest high-tide level, larger stones were common and the gravel gave place to black mud. All stones below *H* were covered with seaweed (*Fucus* spp.).

The upper part of the bed of IV (above *B*) was similar to that of II in consisting of small stones with occasional larger ones resting on coarse gravel. But the region of large stones embedded in black mud started at a much higher

[1] These numbers were arbitrarily chosen since the streams appear to be unnamed.

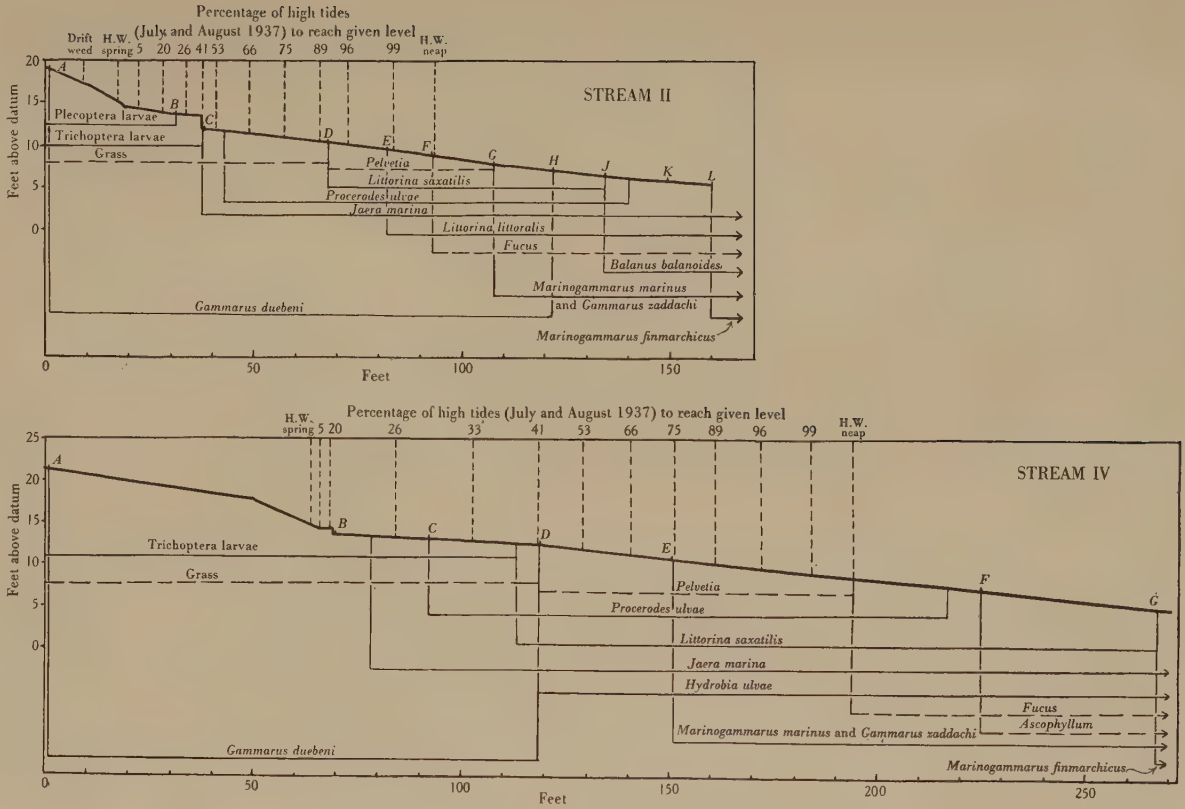
Percentage of high tides (July and August 1937) to reach given level
Drift weed
H.W. spring
5 20 26 41 53 66 75 89 96 99
H.W. neap
STREAM II
Feet above datum
Plecoptera larvae
Trichoptera larvae
Grass
Pelvetia
Littorina saxatilis
Procerodes ulvae
Jaera marina
Littorina littoralis
Fucus
Balanus balanoides
Marinogammarus marinus
and Gammarus zaddachi
Gammarus duebeni
Marinogammarus finmarchicus
Feet
STREAM IV
Trichoptera larvae
Grass
Pelvetia
Procerodes ulvae
Littorina saxatilis
Jaera marina
Hydrobia ulvae
Fucus
Ascophyllum
Marinogammarus marinus and Gammarus zaddachi
Gammarus duebeni
Marinogammarus finmarchicus

Fig. 1

level, namely, at *D*, which was considerably above the lowest high-tide level. From a point a little above *F* the stones were in increasing numbers covered with *Fucus* spp. The higher upper limit of the mud zone in IV in relation to the high-tide levels is probably partly explained as a result of the lesser gradient.

The surveys were not carried to a lower level than that indicated in the figure for the reason that below this the bed of both streams merged into the general level of the shore and no clear watercourse could be defined at low tide.

Table 1

	Average gradient of bed (neap-spring H.W.)	Upper limit	
		Procerodes ulvae	*Jaera marina*
Wembury	1 in 10 (calculated from Pantin, 1931)	Just below H.W. neap	Well below H.W. neap
South Rona, Stream II	1 in 13	Covered by 55% high tides	Covered by 40% high tides
South Rona, Stream IV	1 in 22	Covered by 40% high tides	Covered by 25% high tides

It will be seen that within the limits chosen, the entire ranges of only two species were included, namely *Procerodes* (*Gunda*) *ulvae* and *Littorina saxatilis*. Pantin found that at Wembury the limits of *Procerodes ulvae* were well defined and were identical with those of *Protodrilus flavocapitatus* (not found on South Rona). But he found the upper limit of *Procerodes* to be just below high-water neap level, whereas in both the Rona streams it spread well above this, though it was lower in II than in IV. We may tentatively suggest (see Table 1) that the upper limits of *Procerodes* and of *Jaera* are at least partly determined by the gradient of the stream bed between spring and neap high-water levels. As Fig. 1 shows, the upper limits of most species were higher in IV than in II. In addition to *Procerodes* and *Jaera*, *Littorina saxatilis* and *Marinogammarus marinus* show this clearly. The existence of a "desert zone" devoid of animals in the Wembury stream between spring and neap high-water levels (Pantin) may also be attributable to the steep gradient in this region. It is obvious, however, that no very definite conclusion, on these lines can be arrived at from the data available. But the lowering of the upper limit of a species in a stream with steeper gradient might be expected, since the rate of flow being greater the salinity fluctuations in the water under the stones will be more rapid and extensive.

3. Occurrence and distribution of *Gammarus*

We are much indebted to Mr G. M. Spooner for the identification of the stream and shore *Gammarus*. The new genus *Marinogammarus* includes a group of species which in most previous records from Britain has been referred to as *Gammarus marinus* (Sexton & Spooner, 1940).

It is well known that *Marinogammarus marinus* tends to congregate in the intertidal zone below the mouths of streams. In both our streams its upper

limit coincided with that of *Gammarus zaddachi*. The latter were much dwarfed and of the so-called "hairy" variety, easily confused with *G. duebeni*. The "hairless" variety of *G. zaddachi* was recorded twice from below other streams on South Rona and Raasay. *Marinogammarus obtusatus* was also found between tide marks on both islands, but not below stream mouths.

Gammarus duebeni, a common brackish water species on many parts of the British coast, was found to occupy the upper part of the intertidal zone mainly above the range of *Marinogammarus marinus* and *Gammarus zaddachi*, though overlapping the latter slightly in Stream II. It seems possible that the lower limit of *G. duebeni* is determined more by competition with other species than by physical or chemical conditions, since in the laboratory it can be readily adapted to pure sea water (Beadle & Cragg, 1940).

The most remarkable feature in the distribution of *G. duebeni* was its upper limit. In both streams it penetrated to a vertical distance of about 5 ft. above the spring high-water level which in II was well above the level to which weed had been washed in times of storm. There is no doubt that it was living in permanently fresh water in the upper part of its range. This in itself is not unexpected, since it has now been reported from fresh waters in several parts of Britain and is the common fresh-water species of Ireland (see review by Reid, 1939). The surprising fact is that its fresh-water range was restricted to the lower end of the streams. Such was the case in all of the six streams investigated on South Rona. This contrasts with the observations of Crawford (1937) on a stream at Kynance, Cornwall, where *G. duebeni* was inhabiting the entire course to the height of more than 100 ft. above sea level. Although Forrest *et al.* (1936) recorded *G. duebeni* from the fresh-water lochs of the island of Barra, and Reid (1939) found it in some Irish loughs, it was absent from Loch Braig and the other inland waters of South Rona. It is possible that the composition of the fresh water may determine the extent of penetration by *G. duebeni*.

G. duebeni was also found in several pools close to the shore within the splash zone. The salinity of these as measured by a hydrometer varied from pure fresh water to approximately 120% sea water. It was also found, together with *Talitrus saltator* and woodlice, under heaps of damp washed up weed in the mouth of a small dry water course in Dry Harbour.

On Raasay the distribution of *Gammarus duebeni* was similar. Several streams running into Inverarish Bay and over the shore at Fearns contained *G. duebeni* extending to a little above the highest tide level. No other *Gammarus* were found in any stream nor in the two inland lochs, na Meilich and na Maa. It was therefore remarkable that a third loch, a Chadhacharnaich, was found to contain a dense population of *G. lacustris* G. O. Sars. We are indebted to Dr K. Stephensen of the Copenhagen Museum for a confirmation of our identification. Its occurrence on Raasay is of great interest in that this northern species is common in Norway, where *G. pulex* is unknown. It has

once previously been recorded for the British Isles, from Loch Branahuie in the Outer Hebridean Island of Lewis (Elton, 1937). (Elton refers to this species as *G. pulex* var. *lacustris*, on the basis of Dr Stephensen's naming at that time.) It is therefore desirable that an investigation should be made of the fresh-water *Gammarus* on the mainland of the Highlands. The species *G. pulex* has not as yet been recorded from any of the Hebrides. On Barra, as on South Rona, the only fresh-water *Gammarus* is *G. duebeni* (Forrest *et al.* 1936). There is considerable scope for an investigation of the factors involved in the distribution of the fresh-water species of *Gammarus*, and the Hebrides would form a very suitable field for such work. Elton (1938) records the presence of *Gammarus* (not collected) in two small lochs on the island of Pabbay, at the west end of the Sound of Harris.

We are indebted to Prof. A. D. Hobson for the opportunity to do this work during the University of Durham King's College Expedition to South Rona and Raasay in the summer of 1937, and for his interest and encouragement.

4. Summary

1. A survey was made of the distribution of the fauna in the intertidal zone at the mouths of two streams on the island of South Rona.

2. When these are compared together and with the observations of Pantin at Wembury, it is found that the height of the upper limit of a species in relation to the spring and neap high-tide levels appears to bear an inverse relation to the gradient of the stream bed. The possible significance of this is discussed.

3. *Gammarus duebeni* was found to penetrate into fresh water but was confined to the lower ends of the streams on both South Rona and Raasay.

4. No other *Gammarus* were found in the fresh waters of streams or inland lochs, with the exception of Loch a Chadhacharnaich on Raasay, which contained *G. lacustris*, a northern species once previously recorded for the British Isles on the island of Lewis, Outer Hebrides.

5. List of species mentioned in the text

Platyhelminthes, Turbellaria: *Procerodes* (*Gunda*) *ulvae* (Oerstad).
Annelida, Archiannelida: **Protodrilus flavocapitatus* Uljanin.
Mollusca, Gastropoda: *Littorina saxatilis* (Olivi).
L. littoralis (L.).
Hydrobia ulvae (Pennant).
Crustacea, Amphipoda: *Jaera marina* (Fabricius).
Marinogammarus marinus (Leach).
M. obtusatus (Dahl).
M. finmarchicus (Dahl).
Gammarus zaddachi Sexton.
G. duebeni Lilljeborg.
G. pulex (L.).
G. lacustris G. O. Sars.
Talitrus saltator (Montagu).
Crustacea, Cirrepedia: *Balanus balanoides* (L.).

* Not found on Raasay or South Rona.

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THE ACTIVITY OF CERTAIN ARCTIC INSECTS AT LOW TEMPERATURES

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1. Introduction

The work described in this paper was done at Inari in Finnish Lapland during June 1939. Inari is approximately 69° north latitude and 18° east longitude. A grant received from the Government Grant Committee of the Royal Society made the expedition possible.

Recent work (Mellanby, 1939) has indicated that the results of many of the older experiments on insect activity at low temperatures are liable to be inaccurate because the investigators have disregarded the effects of previous conditions on their insects. I have shown that in a number of cases, the "chill-coma temperature" (i.e. the temperature at which the insect is immobilized by cold) is considerably higher for insects of the same species which have been kept for 24 hr. under warm conditions that it is for other individuals from a cooler environment. This means that insects which have been for a short time under cool conditions are in some way acclimatized and therefore able to move actively at considerably lower temperatures than those from warm. Acclimatization is a fairly rapid process, for after less than 24 hr. the position of the chill-coma temperature may be completely altered. Under fluctuating temperature conditions the chill-coma temperature fluctuates also. When an insect is cooled even slightly below its chill-coma temperature and kept there for a period, no acclimatization takes place, for these processes only occur in that zone of temperature in which activity is possible. The "cold death-point" (i.e. the temperature where cold proves rapidly fatal) is similarly affected by the previous conditions of temperature.

2. Technique

The following species of insects were used:

The stone-fly, *Dictyopterygella subfissa* Bingtsson. Nymphs and adults.
The ant, *Formica rufa* var. *rufo-pratensis* Forel. Adults.
The beetle, *Hylastes ater* Paykull. Adults.
The mosquito, *Aedes punctor* Kirby, Larvae, pupae and adults.
The mosquito, *Theobaldia alaskaensis* Ludlow. Larvae, pupae and adults.

The methods used in these experiments were described in the earlier paper (Mellanby, 1939). The insects, in batches of three to six individuals at a time, were placed in glass flasks immersed in water kept at a low temperature in a vacuum jar. The water was cooled by the addition of ice. The insects were

transferred after acclimatization at a higher temperature to some particular low temperature. This temperature was maintained for a quarter of an hour, and the reactions of the insect at the end of this period was observed. Terrestrial insects were placed in an Erlenmeyer flask, the bottom of which was roughened with sand fixed in wax. For aquatic forms the flask was partly filled with water, and the insects were transferred together with only a small amount of water, insufficient to alter the temperature appreciably. Using these methods, the chill-coma temperature was found to be quite sharply defined, for the insects appeared to be able to move actively at only one or two degrees above the point at which they were completely immobilized. This method unfortunately requires rather large numbers of insects, and in some cases I was only able to determine the chill-coma temperature very approximately.

Before the insects were exposed to the experimental conditions they were maintained at various temperatures for different periods of time. Many were simply removed from their natural environment, the microclimatic conditions of which had been observed. During the whole period of the experiments, meteorological records were kept and these standard figures were correlated with the changing microclimatic conditions of the actual places (e.g. interior of anthills, swamps, etc.) occupied by the insects. During cool weather some of the insects were maintained in a warm room, and during the warm weather steady cool conditions were obtained by submerging vessels in the ice fed river where the temperature remained around 10° C.

3. Climatic conditions at Inari

(*a*) *Macroclimatic conditions*

Inari is more than 100 miles from the nearest sea and has a fairly extreme climate. During the winter it may be as cold as −55° C., and in June we observed temperatures over +30° C. During the winter the insects lie buried beneath the snow and will not be subjected to such low temperatures, but during the summer the direct sun must sometimes warm them considerably over 30° C. (see also Thienemann, 1938). During June when this work was in progress, the "midnight sun" never set, but the temperature was normally always lowest about 2.00 a.m. and warmest around midday and in the early afternoon. At the beginning of the month the weather was fine. At "night" the temperature fell 1–3° below zero and during the day it rose to about 10° C. Between 9 and 16 June it became very wet and temperatures hardly exceeded 10° C., though they never fell to zero. About 16 June a "heat wave" began, and the day temperatures remained at about 30° C. for many hours. 32° C. was the highest recorded in the Stevenson screen. On the 21st it became cool and wet again, the temperature for several days only fluctuating between 3 and 10° C., except that about 2.00 a.m. on the 24th it fell to half a degree below zero for a short time.

(*b*) *Microclimatic conditions*

Enormous differences in temperature were observed in situations only a short distance from one another. Table 1 gives results obtained on four different occasions. It will be seen that on 19 June, the occasion for which I have the most complete records, the range of temperature extended at one time from 0 to 45° C. These figures show that simple records of "Stevenson screen" temperatures may tell us little about the actual conditions experienced by the insects themselves. It is obvious that such figures as "monthly means" without fuller particulars are quite meaningless when applied to the behaviour of the insects.

Table 1. *Microclimatic conditions at Inari, Finnish Lapland, during June* 1939. *All results given in degrees Centigrade*

Hour and date June 1939		Shade temp. (Stevenson screen)	Anthill, 1 cm. below surface	Air among stones near river	River	Stream	Swamp	Snow-drift
1530	8th	8·5	12·0	—	7·0	—	—	0·0
1200	9th	9·0	—	—	7·0	—	12·0	0·0
1400	19th	32·0	45·0	16	10	24	34	0·0
1400	22nd	7·0	—	—	10	—	9·0	0·0

4. Results

As the insects used had been kept under a large variety of conditions it is impossible simply to give the conclusions in a straightforward table without some detailed explanation. The conclusions from each species are given separately in the following sections and the final results are summed up in Table 2.

Table 2. *Approximate chill-coma temperatures of various insects after acclimatization to different temperatures. For details see text*

	Chill-coma temperature (° C.). Acclimatized to 7–12° C.	Acclimatized to 20–30° C.
Stone-fly, *Dictyopterygella subfissa*:		
(*a*) Nymph	<0	<0
(*b*) Adult	<1	>1
Ant, *Formica rufa* var. *rufo-pratensis*:		
(*a*) Adult	1	3
Beetle, *Hylastes ater*:		
(*a*) Adult	1·5	4
Mosquito, *Aedes punctor*:		
(*a*) Larva	<0	<0
(*b*) Pupa	<1	>2
(*c*) Adult	<3	5·5
Mosquito, *Theobaldia alaskaensis*:		
(*a*) Pupa	<2	>2
(*b*) Adult	<4	>4·5

The stone-fly, Dictyopterygella subfissa *Bingtsson*

The nymphs were found in large numbers clinging to stones at the edge of the river Vasko at a time when thousands were leaving the river to emerge as adults. The water temperature was 7° C. Nymphs taken directly from the river were still active at 0° C., others kept for 48 hr. at between 20 and 24° C. were not immobilized by 0° C. This implies that although the specimens kept at the higher temperature may be physiologically affected, the effect is not sufficient to raise their chill-coma temperature above 0° C.

Adults kept at 10° C. were active when cooled below 1° C.; but at this temperature others previously kept at 20–24° C. were immobilized. Thus the adults, unlike the larvae, had their chill-coma temperature altered by a sojourn at a higher temperature.

The ant, Formica rufa *var.* rufo-pratensis *Forel*

One anthill, conveniently situated, provided ample material, and it was possible to use some hundreds of individuals. Soldiers and workers were tested; there appeared to be no difference between the two forms. Individuals were collected outside during the cold weather of early June (temperature below 10° C.) and they had a chill-coma temperature of 1° C. Others, exposed for 24 hr. to 20–22° C., showed a chill-coma temperature of 3° C.

It is interesting to note that, provided the temperature was above 6° C., the whole of the top of the anthill was seen to be covered with active ants at all hours. The sun was above the horizon during the whole 24 hr. and the species showed no diurnal rhythm.

The beetle, Hylastes ater *Paykull*

During the warm weather swarms of these insects were observed flying near the river between 18.00 and 24.00 hr. It was possible to catch 20 individuals with three sweeps of a butterfly net. The chill-coma temperature for beetles kept for 16 hr. at 8–9° C. was approximately 1·5° C. Others kept at 24–30° C. for 48 hr. had a chill-coma temperature of 4° C.

The mosquito, Aedes punctor *Kirby*

This is the commonest Arctic mosquito, and its presence in vast numbers may make life very uncomfortable in many areas. As the spring was rather late in 1939, wild adults hardly appeared at Inari before the end of June. The adults used in these experiments were mostly bred out in a warm room. They did not appear to differ in their physiology from the few wild individuals captured.

(*a*) *Larvae.* This species passes the winter in the larval stage. Abundant specimens were found in the pools at Inari. Under natural conditions during June water temperatures varying between 5 and 34° C. were measured. The larvae were always active when cooled to 0° C., no matter what the previous conditions had been.

(*b*) *Pupae.* By 18 June pupae were abundant in the swamps. One batch was removed from water at 26° C.; it is probable that the water temperature had been above 20° C. for at least 10 hr. These insects were immobilized by 2° C., as also were other individuals kept between 24 and 30° C. for 24 hr. Pupae kept for 24 hr. at 10° C. were still active below 1° C. Other pupae from the pond mentioned above during the cold weather which began on 21 June (by which time the water was in the region of 9° C.) were also active below 1° C. These experiments are sufficient to show that the pupae, unlike the larvae, had their chill-coma temperature readily altered.

(*c*) *Adults.* These adults were bred out from pupae indoors. Individuals kept for 24 hr. at 10° C. were active at 3° C., while individuals kept for 24 hr. at 24–28° C. had a chill-coma temperature of 5·5° C.

A little above the chill-coma temperature the mosquitoes could crawl actively but were unable to fly. The threshold for flying was not determined accurately; it appeared to be in the neighbourhood of 10° C.

The mosquito, Theobaldia alaskaensis *Ludlow*

Unfortunately it was only possible to obtain 12 pupae of this species, and from these only eight adults emerged successfully. The few results obtained are included here for completeness.

(*a*) *Pupae.* Pupae taken directly from the pond whose temperature was 16° C. (the water temperature at this time was rising rapidly due to the sun, and a few hours earlier had only been 10° C.) were fully active at 2° C. Six of these pupae kept for 24 hr. at 22° C. were immobilized at 2° C., though when the temperature rose to 5° C. they were quite active.

(*b*) *Adults.* Four adults were kept at 10-12° C. for 24 hr. and four at between 24 and 30° C. for the same period. At 4·5° C. those from the lower temperature could crawl actively but those from the higher were completely immobilized.

5. Discussion

The results given above show that these insects can be divided into two classes. The first includes those with a chill-coma temperature which cannot be altered by exposure to different conditions. Thus the stone-fly nymphs and the *Aedes* larvae are active at 0° C. whatever the previous conditions to which they have been exposed. The other insects, including the later stages of the stone-fly and the *Aedes*, are more easily immobilized by cold after acclimatization to warm conditions.

I do not think that these results necessarily imply any fundamental difference between the two classes of response. This type of adaptation implies some physiological change in the insect concerned. These and previous experiments show that the degree to which different insects are affected may vary. It may well be that the changes in the stone-fly nymphs and the *Aedes* larvae are simply insufficient to be apparent in these experiments. Possibly if the water were super-cooled, after exposure to high temperatures, these insects would be immobilized only slightly below zero, while other specimens previously kept cool would be active several degrees below zero.

Those forms which are always able to be active at 0° C., no matter what the previous conditions, are those likely to be subjected in the field to low temperatures for considerable periods. In the spring as soon as the snow melts, the *Aedes* larva may well be exposed to fluctuating temperatures (Thienemann, 1938) when their ability always to be active may be valuable. The more advanced stages of the stone-fly and *Aedes* which only appear sometime later, are less likely to be adversely affected by having a higher chill-coma temperature.

6. Summary

1. The effects of acclimatization to different temperatures on the position of the chill-coma temperature of several stages of five species of Arctic insect has been determined in the field.

2. Those stages which are normally exposed to low temperatures for long periods are least easily immobilized by cold, and acclimatization to warm conditions may not raise their chill-coma temperature.

3. The later stages of the same insects which normally occur when it is warm are more easily affected. After exposure to warm conditions the chill-coma temperature is commonly higher than after they have been kept cool.

7. ACKNOWLEDGEMENTS

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THE FOOD OF THE GRAYLING (*THYMALLUS THYMALLUS*), FLOUNDER (*PLATICHTHYS FLESUS*), ROACH (*RUTILUS RUTILUS*) AND GUDGEON (*GOBIO FLUVIATILIS*), WITH SPECIAL REFERENCE TO THE TWEED WATERSHED

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1. Introduction

The chief features, other than spawning habits, which make one species of fish an influential factor in the lives of others in the same habitat, are the kind and amount of food eaten. The literature which deals with food studies in general is extensive and of scattered origin. With the exception of a few papers (e.g. Turner, 1921; Tchougounow, 1919) references to the food of "coarse" fishes are of the most general nature (e.g. Yarrell, 1859; Day, 1880–84; Regan, 1911). In Britain and Ireland the published papers giving detailed accounts of the food of fresh-water fishes have been restricted to the brown trout (*Salmo trutta*), (O'Donoghue & Boyd, 1930, 1932, 1934; Pentelow, 1932; Slack, 1934; Southern, 1935; Allen, 1938; Neill, 1938; Frost, 1939) and the perch (*Perca fluviatilis*), (Allen, 1935). The stomach contents of these and other fishes have doubtless been investigated by fishermen, but the records, if kept, are rarely published.

The present paper deals with the food of fishes belonging to four species which occur in the Tweed watershed. Of these, details of the stomach contents of only the grayling (*Thymallus thymallus* L.) and the roach (*Rutilus rutilus* L.)

have so far been published (Probatov, 1936; Gerrish, 1938, 1939; Tchougounow, 1919). In regard to the other two species of Tweed fishes which have been investigated, the fresh-water feeding habits of the flounder (*Platichthys flesus* L.) have previously been given only superficial attention and the stomach contents of gudgeon (*Gobio fluviatilis* L.) are stated briefly in general works.

The nature of the material from the River Tweed and its tributaries has permitted the presentation of the results, in the case of the grayling and the flounder taken from the River Tweed itself, not only qualitatively but quantitatively. The investigation of the Teviot grayling stomachs has not yet proceeded far enough to permit numerical representation of the contents, but some significant qualitative differences are already apparent. The results of the examination of the roach and gudgeon stomachs, although not as satisfactory as in the case of the grayling and flounder, have been sufficient to form the basis of some conclusions as to the feeding habits of these fish.

2. MATERIAL AND METHODS

The investigation has involved the examination of the stomachs and in some cases the intestines of 227 fish. The Zoology Department of the University of Glasgow has been able to obtain much valuable material from nettings of coarse fish from the River Tweed at Ladykirk, Berwick, in September 1938, the River Teviot below Ancrum Bridge in May 1939, and the River Till at Twizel Bridge also in May 1939.

From the River Tweed 191 grayling and 80 flounders were taken in the deeper mid-regions of the river and 200 roach in a weedy backwater. The stomachs of 50 specimens of each species, and in the case of the roach the intestines also, have been examined for food debris. The River Teviot produced a larger supply of grayling but time has permitted the examination of only seven stomachs of this group. Two hundred roach were collected from the River Till of which the stomachs and intestines of 50 have been examined as well as those of 20 gudgeon collected at the same time.

In connexion with the food of grayling, Dr H. D. Slack of the Zoology Department has kindly provided a series of records of stomach contents from 92 fish taken in the River Test, Hampshire, during March 1935, and from 25 fish taken in Derbyshire in October 1935. The results have been tabulated and included in the present work.

The fish were preserved in formalin within 6 hr. of the time of capture. The grayling were weighed, measured for length and placed in 4% formalin, the stomachs being removed and the contents emptied into vials containing 10% formalin, or in the case of small stomachs preserved entire. The flounder and roach from the Tweed were preserved whole in 4% formalin after the body cavities had been cut open to allow the fluid to penetrate to the viscera. The alimentary canals of the roach and gudgeon from the Till were removed from

the fish and placed in 10% formalin, while the fish themselves were preserved as in the case of the grayling.

At the time of examination an approximate measure of the volume of the stomach contents of the grayling was taken by means of a graduated cylinder. Length measurements were made of the flounders before their stomachs were removed. In other respects the method of examination was the same for the grayling and flounder material. In both cases the stomachs were well filled with food, which had been only slightly affected by the action of the digestive fluids between the time of capture and the preservation of the stomach contents in formalin. The contents were emptied into watch glasses, and records made of the number of individuals of each type of organism occurring in the stomach. The food remains in the roach and gudgeon were scanty in nature, of small size and mainly restricted to the intestine. Samples of the debris in the stomachs and intestines of these two species were suspended in water, and examined with a microscope.

3. Food of grayling (*Thymallus thymallus*)

(*a*) *The Tweed watershed*

For the 50 grayling from the River Tweed and seven from the River Teviot whose stomach contents were investigated, the following data have been obtained:

	Tweed grayling	Teviot grayling
Average length	25·1 cm.	23·6 cm.
Average weight	180 g.	147 g.
Age groups represented	1, 2, 3 yr.	1, 2 yr.
Time of capture	22 September 1938	11 May 1939
Number examined	50	7
Average volume of stomach contents	4·3 c.c.	6·7 c.c.

Although the results are not strictly comparable, there is a significant difference between the volumes of the stomach contents of the two groups. The fish taken in the spring appear to have been feeding more heavily than the September catch as evidenced by the higher average volume of the stomach contents of the Teviot grayling, in which the average length and weight are lower than in the other group. This conclusion is further supported by the fact that the vials containing stomach contents of Teviot grayling not yet examined obviously contain a larger amount of debris than similar vials of Tweed grayling material.

The results from the examination of stomach contents of grayling confirm the statement of Probatov (1936) that the feeding habits of these fish are "exceptionally unfastidious". The bulk of food debris consisted of animal organisms. Vegetable remains occurred in six of the 57 grayling stomachs and included only a few small hard twigs, seeds and fir needles. In two cases a grayling scale was found. Most of the stomachs contained some bottom silt, sand, and in a few there were pebbles up to 7 mm. in diameter.

The animal stomach contents are listed in Table 1. The total number of individuals of all groups is 15,882 with an average of 318 per stomach. It is obvious that the food of the Tweed grayling consists of a wide variety of animals. Some of these occurred infrequently in the stomachs and may be considered of minor importance in the diet. For example, free-living Nematodes, Ostracods and many insects, especially among the Coleoptera, are represented by single individuals in the total of 15,882. This accounts for the extremely small figures for these groups in the percentage column.

Table 1. *Stomach contents of grayling* (Thymallus thymallus) *from the Tweed Watershed. Animals marked * occurred in Teviot grayling; all those with figures occurred in Tweed grayling*

	Number of individuals in 50 stomachs	Percentage of individuals in 50 stomachs	Percentage of stomachs where found
Nematoda	1	0·01	2
***Oligochaeta**	—	—	—
Crustacea			
Ostracoda	1	0·01	2
Amphipoda			
**Gammarus pulex* L.	15	0·09	18
Insecta			
Dermaptera			
Unidentified Forficulidae	3	0·02	6
Forficula auricularia L.	1	0·01	2
Plecoptera			
**Perlodes* sp. nymph	1	0·01	2
**Leuctra* sp. nymphs	46	0·29	52
*Nemura sp. nymphs	—	—	—
Unidentified imagines	4	0·03	8
Odonata			
Aeschnidae nymphs	2	0·01	4
Hemiptera			
Aphelocheirus aestivalis Fab. var. *Montandoni* nymphs	14	0·09	18
*Corixidae imagines	—	—	—
Acanthiidae imagines	2	0·01	4
Capsidae imagines	1	0·01	2
Ephemeroptera			
Rhithrogena sp. nymphs	41	0·26	32
**Ecdyonurus* sp. nymphs	109	0·69	32
Ephemerella sp. nymphs	276	1·74	100
**Baetis* sp. nymphs	2078	13·08	100
Unidentified imagines	3	0·02	6
Trichoptera			
**Rhyacophila* sp. larvae	7	0·04	10
**Glossosoma* sp. larvae	33	0·21	26
Agapetus sp. larvae	1	0·01	2
Polycentropus sp. larvae	1	0·01	2
**Hydropsyche* sp. larvae	81	0·51	68
*Limnophilidae sp. larvae	56	0·35	58
**Plectrocnemia* sp. larvae	—	—	—
Coleoptera			
Agonum sp. imago	1	0·01	2
Nebria iberica Oliv. imago	1	0·01	2
Amara sp. imagines	3	0·02	6
Amara plebia Gyll. imago	1	0·01	2
Loricera pilicornis F. imagines	2	0·01	4
Haliplus fluviatilis Aubé imago	1	0·01	2
Haliplus lineatocollis Marsham imagines	2	0·01	4
Dytiscidae imagines	2	0·01	4

Table 1 (*continued*)

	Number of individuals in 50 stomachs	Percentage of individuals in 50 stomachs	Percentage of stomachs where found
Dytiscidae larvae	1	0·01	2
**Oreodytes halensis* F. imagines	7	0·04	8
Hydrophilidae imagines	1	0·01	2
Cercyon haemorrhous Gyll. imago	1	0·01	2
Hydroporus sp. imago	1	0·01	2
Staphilinidae imago	1	0·01	2
Atheta sp. imago	1	0·01	2
Aphodius sp. imago	1	0·01	2
Aphodius contaminatus Herbst. imagines	3	0·02	6
Phyllotreta undulata Kuts imago	1	0·01	2
*Curculionidae imagines	39	0·25	36
Sitones sp. imago	1	0·01	2
Sitones ononidus Sharp imagines	3	0·02	6
Limnius tuberculatus Mull. imagines	4	0·03	6
**Elmis volkmari* Panz. imagines	21	0·13	24
**Elmis parallelopipedus* Müll. imagines	4	0·03	8
Elmis sp. larvae	10	0·06	18
Elmidae larvae (other than *Elmis* sp.)	2385	15·02	86
*Unidentified imagines	3	0·02	6
Hymenoptera			
Proctotrupidae imagines	4	0·03	8
Cynipidae imago	1	0·01	2
Braconidae imago	1	0·01	2
Ichneumonidae imagines	2	0·01	4
Apidae imago	1	0·01	2
Bombus sp. imago	1	0·01	2
Diptera			
*Tipulidae imagines	4	0·03	6
Tipulidae larva	1	0·01	2
*Bibionidae imagines	4	0·03	8
*Mycetophilidae imago	1	0·01	2
**Simulium* sp. imagines	759	4·78	36
Simulium sp. pupae	362	2·28	56
Simulium sp. larvae	17	0·11	26
*Empididae imagines	—	—	—
Phoridae imago	1	0·01	2
Muscidae imagines	14	0·09	10
*Tabanidae larvae	—	—	—
Leptidae larva	1	0·01	2
*Ceratopogonidae larvae	2	0·01	4
*Chironomidae imago	1	0·01	2
*Chironomidae pupae	1434	9·03	88
*Chironomidae larvae	7918	49·86	98
Unidentified imagines	2	0·01	4
*Unidentified larvae	—	—	—
Arachnida			
*Araneida	1	0·01	2
*Hydracarina	35	0·22	16
Mollusca			
Limnaea sp.	9	0·06	12
**Ancylus fluviatilis* Müll.	20	0·13	22
Unidentified remains	8	0·05	8
Total number of individuals	15,882		

The dominant types in the food are found among the insects, of which the Diptera exhibit the largest numbers of individuals, notably of Chironomid larvae. The Chironomidae represented belong to the two subfamilies, Tanypodinae and Chironominae, the numbers of which were not determined. Coleoptera rank second in importance on account of the large numbers of

larval Elmidae (of genera other than *Elmis*). The Ephemeroptera form an important source of food, chiefly on account of the number of nymphs of *Baetis* sp.—13% of the total number of organisms as compared with 2·7% of other genera.

The remaining groups of insects are represented by even smaller numbers of individuals, but comprise a wide variety indicating the catholic taste of the fish.

Table 2

Types occurring in numbers above 10	Number of individuals	Percentage frequency
Muscidae imagines	14	10
Gammarus pulex	15	18
Simulium sp. larvae	17	26
Ancylus fluviatilis	20	22
Elmis volkmari Panz. imagines	21	24
Glossosoma sp. larvae	33	26
Hydracarina	35	16
Curculionidae imagines	39	36
Rhithrogena sp. nymphs	41	32
Leuctra sp. nymphs	46	52
Limnophilidae larvae	56	58
Hydropsyche sp. larvae	81	68
Ephemerella sp. nymphs	276	100
Simulium sp. pupae	362	56
Simulium sp. imagines	759	36
Chironomidae pupae	1434	88
Baetis sp. nymphs	2078	100
Elmidae larvae	2385	86
Chironomidae larvae	7918	98

In Table 2, the types of animals found in numbers greater than ten in the total contents of 50 stomachs are summarized. The percentage of occurrences of the different types shows a general increase as the number of individuals becomes larger. The most outstanding exception is observed in the case of imagines of *Simulium* sp. where there is a relatively high number of individuals (759) and a low occurrence (36%). This is explained by the fact that one stomach contained 595 *Simulium* sp. imagines, and another 133, while the remainder of occurrences were of small numbers. Nymphs of *Ephemerella* sp. show 100% occurrence, although the number of individuals is only about one-seventh of that of *Baetis* sp. nymphs, which were also of 100% occurrence. Other types, such as pupae of Chironomidae and larvae of Elmidae, which were present in much greater numbers than the *Ephemerella* sp. nymphs, have a frequency in the stomachs of 88 and 86% respectively. Only one stomach of the 50 examined contained no Chironomid larvae, so that, in frequency, Chironomid larvae, and nymphs of *Ephemerella* sp. and *Baetis* sp., may be said to rank equally.

In Table 3, the data have been grouped with respect to aquatic and terrestrial forms. Of the 94·48% of the total numbers of individuals classed as bottom or subsurface aquatics more than half consist of larvae of Diptera. Ephemeroptera nymphs, Coleoptera larvae (of approximately equal rank) and Dipterous pupae form the only other important groups. Terrestrial foods are

composed for the greater part of adult Diptera. A small amount of the food (0·15%) could not be classified to a point which would allow inclusion in any of these categories.

Table 3

Bottom or subsurface aquatic	Percentage of total number of individuals	*Surface (aerial or terrestrial)*	Percentage of total number of individuals
Nematoda	0·01		
Crustacea	0·10	Dermaptera imagines	0·03
Plecoptera nymphs	0·30	Plecoptera imagines	0·03
Odonata nymphs	0·01		
Hemiptera nymphs	0·09	Hemiptera imagines	0·02
Ephemeroptera nymphs	15·77	Ephemeroptera imagines	0·02
Trichoptera larvae	1·13		
Coleoptera larvae	15·09	Coleoptera imagines	0·31
Coleoptera imagines	0·28		
Diptera larvae	49·99		
Diptera pupae	11·31	Diptera imagines	4·95
Hydracarina	0·22	Araneida	0·01
Mollusca	0·18		
Total	94·48	Total	5·37

The stomach contents of the Teviot grayling were, in general, of the same type as those of the Tweed grayling. The list for the Teviot grayling is by no means complete, since only seven stomachs have as yet been examined. For this reason the figures for the Teviot material have not been recorded. However, the investigation has already added a few new groups to the list of grayling foods. The most outstanding addition is that of Oligochaetes. Two of the Teviot stomachs contained large members of the group, one 3 in. and the other 2 in. in length. Among the insects, a new Plecopteran, nymphs of *Nemura* sp., were found, as well as several Corixidae imagines and larvae of *Plectrocnemia* sp. Representatives of two families of Diptera, imagines of Empididae and larvae of Tabanidae, not encountered in the Tweed grayling, occurred in these stomachs.

Certain apparent differences in the results from the Tweed and Teviot grayling foods may be attributed to different seasons of capture as well as to local conditions of habitat. The volume of food in the stomachs of Teviot grayling has been observed to exceed that of the Tweed material. This may be attributed to an increase in feeding activities after the spawning period, although, in general, the animals constituting the food of the grayling taken in the spring were larger than in the September foods, on account of the spring maturation of many types of organisms and the consequent absence of younger immature forms. With regard to the types of organisms, *Gammarus pulex* appeared to be somewhat more common in the Teviot stomachs. Among the insects, still the dominant group, the numbers of Chironomidae larvae were large, 2009 individuals being obtained from the seven stomachs. Chironomidae pupae also occurred in large numbers, while of the imagines of this group, so significantly absent from the Tweed material, 15 were found. Ceratopogonidae

larvae numbered 66 in the seven stomachs, showing a marked increase over the two individuals found in the Tweed grayling. The number of *Baetis* sp. nymphs was 148, but the occurrence was limited to five stomachs. *Ephemerella* sp. nymphs were entirely absent.

(*b*) *Hampshire and Derbyshire*

	Hampshire grayling	Derbyshire grayling
Average length	10 in.	10 in.
Age groups represented	2, 3 yr.	1, 2 yr.
Time of capture	March 1935	October 1935
Number examined	92	25

The number of Derbyshire grayling examined is too small for satisfactory comparison with the results from other grayling, but in any case the figures in the percentage columns of Table 4, pp. 310–311, indicate the dominant types of animals found in the stomach contents. Counts of individuals of each type were not available, although the records included notes on the relative abundance of the types.

The same general type of food as was found in the stomachs of the Tweed grayling prevailed in the Hampshire and Derbyshire specimens. Stones and vegetable remains were present as before. The number of items of animal remains in the diet of the grayling from more southern waters is larger than in the case of those from the north, the Hampshire-Derbyshire list totalling 97, the Tweed list 82. Part of this difference may be accounted for by the slightly more complete classification of the animals in the former, rather than by differences in latitude, but certain outstanding changes may be observed in the list for the two more southerly collections.

The three Isopod species, Collembola, *Ephemera*, *Heptagenia*, *Sialis*, *Planorbis*, and a small fish are all unrepresented in the Tweed material, while the Trichoptera are both more abundant and diverse in type.

From the point of view of abundance of individuals the records indicate that in the Hampshire material *Gammarus pulex* occurred in the largest numbers. Chironomidae pupae and imagines were also abundant and *Baetis* sp. nymphs and *Asellus aquaticus* fairly so. In the Derbyshire material, *Planorbis* sp. was the most abundant type. The contents of one stomach were almost entirely composed of this snail. *Baetis* sp. nymphs were second in importance and sub-imagines were also abundant. There were fairly large numbers of *Simulium* sp. larvae, pupae and imagines as well as *Neuroclepsis* sp. larvae.

(*c*) *Discussion*

The food of the grayling, at least in the three areas from which collections have been made, embraces a wide variety of animal organisms, mostly obtained from the bed of the river or streams, but with occasional representatives of surface foods.

Table 4. *Stomach contents of grayling from Hampshire and Derbyshire*

	Hampshire Grayling		Derbyshire Grayling	
	Number of occurrences	Percentage of occurrences	Number of occurrences	Percentage of occurrences
Hirudinea				
Glossosiphonia sp.	4	4·4	2	8
Unidentified leeches	1	1·1	1	4
Crustacea				
Ostracoda	—	—	1	4
Cypris sp.	3	3·3	—	—
Isopoda				
Asellus aquaticus L.	49	53·3	—	—
Asellus meridianus Rac.	1	1·1	—	—
Porcellio sp.	1	1·1	—	—
Amphipoda				
Gammarus pulex L.	70	76·1	11	44
Insecta				
Collembola				
Sminthuridae imago	1	1·1	—	—
Entomobryidae imagines	2	2·2	—	—
Poduridae imago	1	1·1	—	—
Ephemeroptera				
Ephemera sp. nymphs	—	—	4	16
Heptagenia sp. nymphs	2	2·2	—	—
Ephemerella sp. subimagines	11	12·0	2	8
Ephemerella sp. nymphs	10	10·9	4	16
Baetis sp. imagines	—	—	7	28
Baetis sp. subimagines	7	7·6	8	32
Baetis sp. nymphs	29	31·6	16	64
Megaloptera				
Sialis sp. larvae	2	2·2	11	44
Hemiptera				
Corixidae nymphs	—	—	2	8
Sigara sahlbergi Fieb. imago	—	—	1	4
Sigara striata Fieb. imagines	2	2·2	11	44
Trapezonotus sp. imago	—	—	1	4
Lygaeidae imago	—	—	1	4
Unidentified fragment	—	—	1	4
Cercopidae imagines	—	—	3	12
Aphidae imagines	—	—	7	28
Trichoptera				
Rhyacophilidae larvae	16	17·4	—	—
Agapetus sp. pupae	2	2·2	—	—
Agapetus sp. larvae	8	8·7	—	—
Hydroptilidae larvae	2	2·2	1	4
Psychomyidae larvae	9	9·8	1	4
Polycentropidae larvae	18	19·6	—	—
Neuroclepsis sp. larvae	—	—	4	16
Hydropsyche sp. larvae	1	1·1	3	12
Limnophilidae larvae	3	3·3	1	4
Odontocerum sp. pupa	—	—	1	4
Odontocerum sp. larvae	3	3·3	1	4
Molanna sp. larva	1	1·1	—	—
Sericostoma sp. larvae	2	2·2	—	—
Goera sp. larva	—	—	1	4
Brachycentrus sp. larva	—	—	1	4
Leptoceridae larvae	2	2·2	—	—
Mystacides sp. larva	—	—	1	4
Unidentified imago	—	—	1	4
Unidentified pupae	—	—	6	24
Unidentified larvae	—	—	2	8
Lepidoptera larvae	1	1·1	2	8
Coleoptera				
Chrysomelidae imago	1	1·1	—	—
Carabidae imagines	2	2·2	1	4
Haliplidae imago	—	—	1	4

Table 4 (*continued*)

	Hampshire Grayling		Derbyshire Grayling	
	Number of occurrences	Percentage of occurrences	Number of occurrences	Percentage of occurrences
Dytiscidae larvae	2	2·2	3	12
Hydroporous sp. imagines	2	2·2	—	—
Staphilinidae imagines	2	2·2	2	8
Scarabeidae imagines	—	—	2	8
Histeridae? imagines	—	—	1	4
Diversicornidae imagines	1	1·1	1	4
Hydradiphagidae imago	—	—	1	4
Clavicornidae imago	—	—	1	4
Curculionidae imago	1	1·1	—	—
Elmis aeneus Müll. larvae	3	3·3	—	—
Unidentified imagines	1	1·1	3	12
Hymenoptera				
Tenthredinidae imago	—	—	1	4
Tenthredinidae larva	—	—	1	4
Braconidae imagines	—	—	7	28
Figitidae imagines	—	—	4	16
Formica sp. imagines	—	—	3	12
Diptera				
Tipulidae larvae	3	3·3	1	4
Dicranota sp. larvae	6	6·5	—	—
Bibionidae imago	1	1·1	—	—
Simulium sp. imagines	8	8·7	9	36
Simulium sp. pupae	9	9·8	9	36
Simulium sp. larvae	48	52·2	7	28
Athericera imagines	2	2·2	5	20
Borboridae imagines	11	12·0	1	4
Tephrochlamys canescens imago	1	1·1	—	—
Helomyzidae imago	—	—	1	4
Eristalis sp. imago	1	1·1	—	—
Brachycera imago	—	—	1	4
Scatophaga stercoraria L. imagines	—	—	4	16
Ceratopogonidae larvae	4	4·4	—	—
Chironomidae pupae and imagines	66	71·7	—	—
Chironomidae pupa	—	—	1	4
Chironomidae larvae	60	65·2	6	24
Nematocera imagines	—	—	2	8
Unidentified imagines	—	—	2	8
Unidentified larvae	2	2·2	—	—
Arachnida				
Araneida	4	4·4	—	—
Hydracarina	4	4·4	—	—
Mollusca				
Planorbis sp.	1	1·1	20	80
Physa fontinalis L.	1	1·1	—	—
Valvata sp.	1	1·1	—	—
Bithynia tentaculata L.	2	2·2	—	—
Limnaea sp.	—	—	3	12
Pisidium sp.	12	13·0	2	8
Pisces				
Small fish (*Phoxinus*?)	—	—	1	4

The dominant types occurring in the stomachs appear to depend on their availability rather than on selection by the fish, and vary to some extent in different areas. Probatov (1936), in his studies of grayling of the River Kara, found that "in the middle course of the Kara the predominant foods of the grayling are Trichoptera larvae and Ephemeridae, in the mouth of the Kara, [Crustacea] *Mesidothea entomon* and *Pontoporeia affinis*". Gerrish (1939) states

that "in any given season trout and grayling rarely if ever choose the same things as their basic food". In one year Lambourn trout were feeding on shrimps while the grayling stomachs contained mainly caddis larvae. The next year the trout were feeding on caddis larvae or aquatic nymphs and the grayling on shrimps. In an earlier paper (Gerrish, 1938) it was stated that where snails are the dominant food and eaten extensively by the trout, few grayling stomachs have been found to contain many snails.

The Hampshire grayling stomach contents agree with the statements of Probatov and Gerrish concerning Crustacea, *Gammarus pulex* supplemented by *Asellus aquaticus*, forming the most important part of the food.

Gammarus is abundant in the area from which the Hampshire grayling were collected. In the Tweed area no such abundance was apparent, while forms like *Ephemerella*, *Baetis*, probably of equal frequency in all three areas, show a higher percentage in the Tweed grayling on account of the shortage of shrimps. *Hydropsyche* constitutes a relatively higher fraction of the Tweed fauna, as it does of the Tweed grayling food. Of the three districts, *Ephemera* occurs only in the one from which it is recorded as a food element. So far, therefore, the evidence upholds the theory of availability.

On the other hand there is less convincing evidence for this theory in the case of the large quantities of *Planorbis*, in the Derbyshire material, where it was not the most numerous species in the stream; and the small numbers of Elmidae in the Hampshire stomachs, which are less than would be inferred from the strength of the *Elmis* population in the river.

There is an indication here of selectivity on the part of the fish. On balance, however, the results show that the more readily available the food organism the more frequently it is taken by the grayling. The wide range in taste of this fish is well shown by the records, since the food extends from minute Collembola to the occasional ingestion of small fish.

At present, little can be said about seasonal changes in the food of grayling. From the available data it is seen that fish taken from the Tweed waters in September and in May were feeding heavily. The spring group, just past their spawning period, appear to have been feeding somewhat more heavily than the fish taken in the autumn. The extent to which feeding is affected before the spawning period is not known.

4. Food of flounders (*Platichthys flesus*) from the River Tweed

The presence of the flounder in rivers at some distance from the sea and above tide-level has often been recorded. Smitt (1893) describes the fresh-water occurrences of this species in Scandinavian waters and states that not only does it ascend rivers and become completely acclimatized to fresh water, but makes its way into the lakes and breeds there. Similar occurrences are

recorded for Germany, Belgium, France and the British Isles. The literature contains general statements of the food of flounders in their marine habitat. Regan (1911) says that they feed on worms, little fish and other animal forms, but mainly on Crustaceans and Molluscs. That the species feeds while in fresh water has been established. According to Jenkins (1925) the flounder's migration to the rivers is for the purpose of obtaining food, and Lebour (1920) states that young metamorphosed flounders occur habitually in large numbers up the rivers, their food being chiefly small Crustacea. No detailed accounts of the fresh-water foods are available.

From the examination of the stomach contents of 50 flounders of average length 17·6 cm. taken in the River Tweed in September, the information given in Table 5, below, was obtained. The same general types of organisms as were present in the stomachs of Tweed grayling occurred in the flounders. The most significant differences lie among the insects. Here the number of subdivisions of the various orders is extremely limited in comparison with those in the grayling. The numerous adult types of Coleoptera and Diptera are

Table 5. *Stomach contents of flounders from the River Tweed*

	Number of individuals in 50 stomachs	Percentage of individuals in 50 stomachs	Percentage of stomachs where found
Oligochaeta	65	0·74	6
Hirudinea			
Glossosiphonia sp.	1	0·01	2
Crustacea			
Amphipoda			
Gammarus pulex L.	2	0·02	4
Insecta			
Plecoptera			
Perlodes sp. nymphs	1	0·01	2
Chloroperla sp. nymph	1	0·01	2
Leuctra sp. nymph	1	0·01	2
Hemiptera			
Aphelocheirus aestivalis Fab. var. *Montandoni* nymph	1	0·01	2
Ephemeroptera			
Ecdyonurus sp. nymphs	13	0·15	12
Coenis sp. nymphs	3	0·03	6
Baetis sp. nymphs	28	0·32	38
Trichoptera			
Glossosoma sp. larva	1	0·01	2
Plectrocnemia sp. larvae	2	0·02	4
Polycentropus sp. larvae	6	0·07	10
Hydropsyche sp. larvae	6	0·07	2
Limnophilidae larvae	2	0·02	4
Coleoptera			
Elmidae larvae	31	0·35	28
Diptera			
Simulium sp. pupae	2	0·02	4
Simulium sp. larvae	2	0·02	4
Chironomidae pupae	743	8·46	88
Chironomidae larvae	7791	88·87	96
Arachnida			
Hydracarina	3	0·03	6
Mollusca			
Limnaea sp.	2	0·02	4
Ancylus fluviatilis Müll.	59	0·67	36
Pisces	1	0·01	2

absent, these groups being represented only by the immature and definitely subsurface forms. The food list consists entirely of bottom-dwelling animals, as would be expected from the structure and habits of the fish.

The most outstanding feature of the stomach contents is the predominance of immature Chironomidae; indeed the flounders may be said to have been feeding almost entirely on these, as opposed to the small Crustacea referred to by Lebour. *Baetis* sp. nymphs, Elmidae larvae and *Ancylus fluviatilis* were fairly well distributed throughout the stomachs, although the numbers found were quite small. One of the stomachs contained a large number of Oligochaeta.

The most apparent differences between the foods of grayling and flounder are, first of all, in the case of the flounder, the absence of adult types of insects or surface foods such as were found in the grayling stomachs, and secondly, the large numbers of Chironomid larvae with relatively small amounts of other bottom types of larger size, such as *Baetis* sp. nymphs and Elmidae larvae. From the numbers of these last in the grayling stomachs they must have been fairly abundant in the river. Occasionally, specimens of *Baetis* sp. nymphs and *Ancylus fluviatilis* occurred in the larger flounders, but for the most part those of medium and small size contained nothing but Chironomidae. The selection of so many smaller organisms, chiefly Chironomid larvae and pupae, by the flounders, may be attributed partly to the small size of their mouths, partly to their feeding habits, and partly to the relative activity of the food organisms. The contents of the grayling stomachs have given ample evidence that a great variety of bottom foods were available in the Tweed. It is probable that the small-mouthed and relatively slow-moving flounders were unable to capture many of the stronger, swifter animals and were forced to subsist on the more inactive Chironomidae.

5. Food of roach (*Rutilus rutilus*) from the Tweed watershed

Of the 50 fish of average length 19·7 cm. from the September Tweed collection which were examined, the stomachs of all contained only indistinguishable masses of cells. In 20 cases only there was identifiable food debris in the intestines. This was a soft, greenish mass beginning usually just beyond the pylorus and consisting almost entirely of vegetable remains, with occasionally small animals scattered through it. The types of plants and animals observed during the course of the examination are shown in the table on p. 315.

The greater part of the remains consisted of masses of *Oedogonium* along with a great many diatoms, of which *Melosira* was the most abundant. *Cladophora* and some genera of diatoms, such as *Fragilaria*, *Cocconeis* and *Navicula* were fairly abundant. The remainder of the plant types and the animals were found only occasionally.

The stomachs of a similar group of 50 roach of average length 19 cm. taken from the River Till in May were examined. In this case all the stomachs

contained at least a small amount of food. In 13 the algal remains were abundant, while in the remaining 37 there were relatively few distinguishable cells. Much unidentifiable material occurred along with the vegetable remains. The intestines of these roach all contained some vegetable debris. Animal remains were very rare, and consisted of only Chironomidae larvae and pupae. The plant remains included almost all the types as given for the River Tweed roach, except *Oedogonium* which was absent. The dominant type in the Till roach was *Cladophora* and two additional genera of diatoms, *Rhopalodia* and *Cymatopleura*, were noted.

Plant remains			Animal remains
Ankistrodesmus	*Cosmarium*	*Cocconeis*	**Protozoa**
Scenedesmus	*Staurastrum*	*Navicula*	Rhizopoda
Coelastrum	*Melosira*	*Gyrosigma*	*Arcella*
Ulothrix	*Cyclotella*	*Gomphonema*	*Difflugia*
Microspora	*Stephanodiscus*	*Cymbella*	**Crustacea**
Cladophora	*Tabellaria*	*Amphora*	Cladocera
Coleochaete	*Meridion*	*Nitzschia*	*Chydorus*
Oedogonium	*Diatoma*	*Merismopedia*	Ostracoda
Spirogyra	*Fragilaria*	*Oscillatoria*	Copepoda
Mougeotia	*Synedra*	*Nodularia*	*Cyclops*
Micrasterias	*Ceratoneis*	Bits of leaves and stems of higher plants	Copepod nauplius
			Insecta
			Diptera
			Chironomidae larvae
			Arachnida
			Hydracarina

Previously published records of the feeding habits of the British variety of roach have been of a general nature, as that of Regan (1911) who includes weeds, insects, insect larvae, little shellfish and surface flies in the diet. Tchougounow (1919) found that in the case of the Caspian roach (*Rutilus rutilus caspicus* Jak.) the relative amounts of animal and vegetable remains vary with the season. When the roach moves into the shallow parts of the river just before spawning the feeding decreases and the stomach contents are almost entirely vegetable remains, due to the "rich spring flora and relatively poor fauna" of the river shallows. After spawning the fish move downstream into deeper water to renew their strength by consuming Crustaceans and Molluscs. After June, feeding again diminishes gradually until in September and October when the fish return to winter up the river the consumption of vegetable and inorganic materials becomes relatively larger.

The results for the two groups of roach from the Tweed watershed conform to a large extent to these statements made by Tchougounow. The roach taken from the Till in May were in the midst of their spawning season. Those taken from the Tweed itself in September were caught in a shallow, weedy backwater. Both groups had been feeding mainly on plants, the Till roach more extensively than those from the Tweed, the proportion of animal remains being larger in the latter. The decrease in feeding activity appears more pronounced in the Tweed roach where only 20 contained any definable material, while the Till roach all contained some distinguishable organisms.

6. Food of gudgeon (*Gobio fluviatilis*) from the River Till

The 20 gudgeon taken in May had an average length of 16 cm. The food remains were for the most part found in the intestines. Few stomachs contained anything more than an indistinguishable mass of cells. In two cases both plant and animal remains occurred. With regard to the intestinal contents, 12 contained mostly plant debris, six mostly animal, and two only masses of indistinguishable cells with a few scattered animal remains.

The plant remains were of the same type as in the stomachs of the Till roach, with a predominance of *Cladophora* and diatoms. There was a much larger proportion of animal remains than in the case of the roach. The types of animals represented were: *Coenis* sp. nymphs, Limnophilidae larvae, Elmidae larvae, *Simulium* sp. larvae, pupae and imagines, Chironomidae larvae and pupae, Ceratopogonidae larvae, and several unidentified Dipterous larvae.

Previous records of the food of the gudgeon have been of a general nature. Jenkins (1925) states that it is a bottom-living fish, Yarrell (1859) that it feeds on worms, aquatic insects, insect larvae, small Molluscs, ova, and small fry, and Day (1880–84) that it eats some plants as well as animals, but is a capricious feeder.

The stomach contents of the Till gudgeon tend to conform to the last statement, although the bulk of the food debris was, in many cases, of plant origin. The feeding of the gudgeon, like that of the Till roach, had, in all probability, decreased with the approach of the spawning period.

7. Summary

1. Grayling (*Thymallus thymallus*) from the River Tweed (Berwickshire), Derbyshire and Hampshire, taken in March, May, September and October, were feeding heavily on a great variety of animal organisms.

2. In the stomach contents of grayling taken in the River Tweed in September, Chironomid larvae and pupae constituted half the total number of individuals, while *Baetis* sp. nymphs, Elmidae larvae, and *Simulium* sp. pupae and imagines were important groups.

3. Bottom foods comprised 94·5% of the stomach contents of Tweed grayling, surface foods 5·4%.

4. Grayling taken in the River Teviot in May were feeding on the same types of organisms as the September grayling, though more extensively.

5. The stomach contents of Hampshire grayling taken in March were composed chiefly of *Gammarus pulex*, with fairly large numbers of Chironomid pupae and imagines, *Baetis* sp. nymphs and *Asellus aquaticus*.

6. In Derbyshire grayling taken in October, *Planorbis* sp. was the dominant food. *Baetis* sp. nymphs, *Simulium* sp. larvae, pupae and imagines, and *Neuroclepsis* sp. larvae were fairly abundant.

7. The food of flounders (*Platichthys flesus*) in the Tweed consisted almost entirely of Chironomid larvae and pupae. Small numbers of other animals were found, but the fish appear to be restricted to small, inactive organisms by the size of their mouths, their feeding habits and their inability to move swiftly.

8. Roach (*Rutilus rutilus*) taken in September and in May were feeding, though not extensively, on plants, chiefly *Oedogonium*, *Cladophora*, and diatoms. Animal organisms were rarely found.

9. In spring and autumn roach occur in the shallow, weedy regions of rivers and the proportion of vegetable debris in the stomachs is correspondingly great. It seems reasonable to suggest that the feeding of roach depends on the seasons.

10. Gudgeon (*Gobio fluviatilis*) taken in the River Till in May were found to be feeding to a limited extent on plants of the same type as those found in the stomachs of the roach, and on some bottom-living animals. Feeding is probably affected by the approach of the spawning period.

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FURTHER OBSERVATIONS ON THE COLONIZATION OF A NEW ROCKY SHORE AT PLYMOUTH

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1. Introduction

In 1935 a concrete wall and beach of new stone were made at Tinside, Plymouth. An account of the colonization of these during their first two years has been given in an earlier paper (Moore, 1939), and at the same time the fauna and flora of a neighbouring old-established beach were described for comparison. The present paper comprises a review of conditions on the new beach and wall in November 1939; about four years after they were made.

We wish to express our indebtedness to all those to whom we have referred specimens for identification: Mr L. R. Crawshay (Sponges), Dr M. V. Lebour and Dr V. Fretter (Molluscs), Mr W. J. Rees (Hydroids), Mr G. M. Spooner (Amphipods), Mr G. A. Steven (Ascidians), Mr D. P. Wilson (Polychaetes) and Miss M. F. Mare (Algae).

2. Status of the flora and fauna in 1939

An asterisk after a species indicates that it had not been recorded from the beach in August 1937. The nomenclature used throughout is that of Knight & Parke (1931) and The Plymouth Marine Fauna (Mar. Biol. Ass. U.K. 1931).

ALGAE

Fucus serratus L. Well grown and abundant on rocks on the beach, and generally distributed but less abundant on the lower zones of the wall. In 1937 it was found on the wall only in those parts kept damp by the outfall from the pool.

F. vesiculosus L. Moderately common on the wall, and showing little change since 1937. Not present on the beach.

Pelvetia canaliculata Dene et Thur. Two small tufts, the larger about 5 cm. long, at a high level on the wall. One non-persistent tuft recorded in the same habitat in 1937.

Ascophyllum nodosum Le Jol.* A few patches with fronds up to about 17 cm. long on the wall. None of the fronds with more than one bladder.

Laminaria digitata Lamour. A few small plants near low water, and one on the wet part of the wall. Except for the latter, there is little change since 1937.

Cladostephus spongiosus Ag.* Locally common at low water.

Sphacelaria sp.* Confined to the wet seepage areas of the wall, where it forms a felt similar to the *Enteromorpha* felt on the dryer parts. This may have been missed in the earlier surveys.

Corallina officinalis L.* Several patches on parts of wall kept wet by seepage.

Chondrus crispus Stackh.* A few patches near low water.

Rhodymenia palmata Grev. Abundant and well grown near low water. Moderately common but smaller on wet parts of the wall, where it has appeared since 1937.

Laurencia pinnatifida Lamour.* A little on a wet patch on the wall.

Porphyra umbilicalis Kutz. Small plants a few cm. long, common in the algal felt on the wall, but not nearly as large or as common as in 1937. This may, however, represent a new growth subsequent to death of the larger plants by desiccation during the summer.

Ulva lactuca L. Condition similar to *Porphyra umbilicalis*.

Enteromorpha sp. Comprising a large part of the algal felt on the wall as in the earlier stages of colonization, but the area of this felt has been considerably reduced by the browsing of limpets.

PORIFERA

Leucosolenia complicata (Mont.).* Fairly common on lower beach: young specimens. Many of the following may have been overlooked on previous occasions as this list is the result of a detailed examination of the material from the present survey by Mr Crawshay.

Sycon ciliatum (Fabr.).* One young only. *S. coronatum* (Ellis & Soll.) was not seen in 1939 though a few were recorded in 1936 and 1937.

Grantia compressa (Fabr.). A few small ones were taken under rocks in 1936, but not in 1937. In 1939 it was a little more abundant though by no means as common as on the old beach; it had spread in small numbers to the wet areas of the foot of the wall. Several in the latter situation reached a length of 2 cm. It is possible that it is rather late in the season for this species to be abundant, since it may have been dying down for the winter.

Halichondria panicea (Pallas). This species was already present in small numbers under rocks near low water in 1937. Well-grown masses are now common under stones and in regions on the sides of larger boulders which are sheltered by fucoids. It is also present in wet areas at the foot of the wall. The following, previously unrecorded, are from Mr Crawshay's report.

Halichondria sp. (*a*).* Two as low spreading cushions: one with embryos.

Halichondria species (about four different species). Many, as irregularly investing or partly lobate patches, from very small up to about 40 mm. in basal extent.

Reniera sp.* (Probably *R. indistincta* Bow.) Many, as small cushion-like patches about 4–10 mm. in maximum extent.

Esperella lobata (Mont.).* Many; especially numerous locally on stones near low water; as small broadly coniform or bulb-like growths, chiefly about 3–6 mm. basally by 4–5 mm. in height.

Chalina gracilenta Bow.* Common locally on wet area near base of wall.

Microciona atrasanguinea Bow.* One only: a thin investment about 30 mm. in maximum extent.

Hymeniacidon caruncula Bow.* Common: irregular massive growths up to 35 mm.

Halisarca dujardinii Johnst.* Common: ranging from very small to about 20 mm.

COELENTERATA

Dynamena pumila (L.). Abundant on stones etc. on the beach, and also on the wetter parts of the wall. This was one of the earlier colonizers and shows little change.

Obelia geniculata (L.).* Common on stones etc. near low water. This may have been missed in the earlier surveys.

Kirchenpaueria pinnata (L.).* Condition similar to that of *Obelia*.

Actinia equina L. Three or four, with discs about 1 cm. diameter, under stones near low water. There is a previous record of one small specimen in 1936.

Anemonia sulcata (Penn.).* One specimen with a disc about 3 cm. diameter under a stone near low water.

Sagartia sp.* One specimen with a disc about 5 mm. in diameter under a stone near low water.

Metridium senile (L.).* One specimen with a disc about 3 cm. diameter under a stone near low water.

ANNELIDA, POLYCHAETA

Nereis pelagica L. Not uncommon in muddy gravel under stones near low water. Young individuals were recorded from this habitat when the gravel first began to accumulate in 1937.

Perinereis cultrifera (Grube).* One specimen in the same habitat.

Arenicola branchialis Aud. & Edw.* Two specimens in the same habitat.

Lepidonotus squamatus (L.).* Two specimens under stones near low water.

Lagisca extenuata (Grube).* Not uncommon in the same habitat.

Pomatoceros triqueter (L.). Common under stones, but has decreased in numbers near low water, where it has apparently been excluded to some extent by the recent growth of sponges and ascidians. It has also extended its range to the damp parts of the wall where it is locally abundant.

Spirorbis borealis Daudin. Distribution similar to *Pomatoceros*.

ECHINODERMATA

Asterias rubens L.* A young specimen about 1 cm. diameter, under a stone near low water.

Amphipholis squamata (Della Chiaje). Present on the under sides of stones embedded n muddy gravel near low water, but seems less common than in 1937.

INSECTA

Lipura maritima Guérin.* A few on the dry upper parts of the wall. It was probably missed in the earlier surveys.

CRUSTACEA

Balanus balanoides (L.). Probably owing to the clearing of the algal felt from large areas on the wall by limpets, this barnacle has increased considerably in numbers since 1937, so that its population in 1939 was quite as dense on the wall as on the neighbouring reefs. 1939 spat were patchy in distribution, and only locally abundant.

B. perforatus Brug. Some individuals on the lower beach have grown to about 26 mm., but there is little change in abundance. It has also spread in moderate numbers to the upper beach and damp lower parts of the wall.

B. crenatus Brug.* In small numbers under stones near low water, and up to about 10 mm. long. One or two also on the lower parts of the wall.

Chthamalus stellatus (Poli). Has increased in numbers since 1937, and on the upper parts of the wall has become quite as common as *B. balanoides*, and has grown to full size for the locality. 1939 spat abundant.

Verruca stroemia (O. F. Müller). A few under stones near low water and fully grown, but showing no increase in numbers since 1937. It is usually restricted to low levels, and has shown no tendency here to spread up the shore.

Gammarus obtusatus Dahl.[1] Mature and immature individuals, some of the former breeding, sparsely distributed under stones on the upper beach. Less common than on a neighbouring beach on the seaward side of the bathing pool.

Melita palmata (Mont.).[2] Locally common under stones at the upper and middle levels of the beach, but not found at low water.

M. hergensis Reid (Reid, 1937).[2] Distribution as above, and nearly as plentiful.

Maera grossimana (Mont.).[2] Two males under stones on the upper beach.

Hyale nilssoni (Rathke).[1] Two specimens, at a fairly high level on the wall, among fucoids.

[1] *G. marinus* Leach was recorded from the old beach, but Mr G. M. Spooner and Mrs E. W. Sexton, who are at present working on the Plymouth species of *Gammarus*, found only *G. obtusatus* there in 1939.

[2] The Amphipods of the new beach have not previously been carefully examined.

Porcellana platycheles (Penn.). This was the first of the two species of *Porcellana* to colonize the shore, and in 1937 was much the commoner of the two. In 1939 it was much less common than *P. longicornis* and actually appeared to have decreased in numbers, being present only in very small numbers at low water. Such a decrease might be due to a winter migration of *P. platycheles* away from the intertidal zone, but it seems unlikely, as we have not observed evidence of it on any other shore.

P. longicornis (L.). Comparatively common under stones near low water, where it seems partially to have replaced *P. platycheles*, and extending to a higher level on the beach than the latter; it has increased considerably in numbers since 1937.

Carcinus maenas (Penn.). Shows little change in abundance, but has spread since 1937 to the damper parts of the upper beach close to the wall. No large specimens were seen, but these may be caught by children.

Pilumnus hirtellus (L.).* Not uncommon under stones near low water.

MOLLUSCA

Gibbula umbilicalis (da Costa). Was a later colonizer of the beach than *G. cineraria*, but was increasing in abundance in 1937, and by 1939 was as common as the latter. It has also extended its range to the top of the beach, and in small numbers to the damp parts of the lower wall.

G. cineraria (L.). Shows little change since 1937 except for extending its range to the upper beach.

Littorina littorea (L.).* In very small numbers under stones and on the lower part of the wall. No young of the 1939, and only one of the 1938 broods were found, the rest being in their third or later year. It seems most likely that these large individuals have migrated onto the beach and not grown up there.

L. rudis (Maton). Shows little change on the wall, where it is abundant in crevices. None seen on the beach.

L. littoralis (L.) [=*L. obtusata* Lam.]. Sparsely distributed on fucoids and under stones but no large specimens seen. Little change since 1937. Present in small numbers in crevices and in empty barnacle shells on the wall.

L. neritoides (L.). Abundant in a very narrow zone on the upper wall, but showing little change since 1937.

Cingula cingillus (Mont.). Seems almost to have disappeared from the beach since 1937 when it was very abundant.

Nucella lapillus (L.) [=*Purpura lapillus* L.].* A few large individuals, mostly mature, under stones throughout the beach, and one young 4 mm. high, at low water. Much less common than on the neighbouring beaches.

Nassarius incrassatus (Ström).* Locally common under stones at low water; and fully grown.

Patella vulgata L. (including var. *intermedia* and var. *depressa*). Has increased considerably both on the rocks and on the wall, but it is larger on the latter where specimens of 5·5 cm. long were recorded.

Patina pellucida (L.).* One under a stone at low water. It may have been detached from *Laminaria* which is abundant below this level.

Emarginula fissura (L.).* One under a stone in the wet area at the foot of the wall.

Goniodoris nodosa (Mont.).* Two, under stones near low water.

Jorunna tomentosa (Cuv.).* Two under stones near low water.

Eolis sp.* One small one under a stone near low water.

Heteranomia squamula (L.). Present under stones near low water, but considerably less common than in 1937, having probably been displaced by the rapidly growing sponges and

[1] The Amphipods of the new beach have not previously been carefully examined.

ascidians. It shows no change in maximum size, this being apparently attained here within a year of settling.

Paphia rhomboides (Penn.) [=*Tapes virginea* L.].* Two small specimens, 10–15 mm. long, in muddy gravel near low water.

Mytilus edulis L. Specimens up to about 10 mm. long in small numbers under stones, but none as large as in 1937. Has also spread to the wall where a few up to 25 mm. long were found in crevices. The general appearance is of young, and not of stunted mussels, which suggests that they do not survive for long on this beach.

Chlamys distorta (da Costa).* One under a stone near low water.

ECTOPROCTA

Lepralia pallasiana (Moll.). Abundant under stones, and has extended its range to damp parts of the wall. This species was abundant on the beach in the earlier surveys, when it was included under *Membranipora* sp.

Membranipora pilosa (L.). Abundant on fucoids near low water.

TUNICATA

Dendrodoa grossularia (van Beneden).* Abundant under stones near low water, where it appears to have displaced to a considerable extent the earlier colonizing *Heteronomia*, *Pomatoceros* and *Spirorbis*. Large numbers of larvae were being liberated on 28 November.

Botryllus schlosseri (Pallas). Shows little change since 1937 except for extending its range to the damp parts of the lower wall.

Botrylloides leachi Sav. Distribution similar to *Botryllus*.

Diplosoma listerianum (Milne-Edw.).* A little under stones at low water.

Distomus variolosus Gaertner.* Fairly common under stones at low water.

PISCES

Blennius gattorugine Bloch,* *B. pholis* L.,* *Ctenolabrus rupestris* (L.).* Single specimens taken under stones near low water.

3. Discussion

The changes in physical and biological conditions on the new beach may best be considered in three sections: the **wall**, the **stony beach** and the **gravel substratum**.

Physically, the **wall** shows some increase in cracks which afford shelter to small Littorinas, but its most marked change is the development of several areas on its lower face which are kept permanently wet by seepage of sea water through from the swimming pool. A few species have appeared in these wet areas and not elsewhere on the shore, while others which were previously restricted to the lower levels of the beach have now extended their range to these wet parts of the wall. Among the former are *Laurencia* and *Corallina*, and among the latter *Pomatoceros*, *Spirorbis*, *Lepralia*, *Balanus perforatus*, *Botryllus*, *Botrylloides*, *Halichondria* and *Rhodymenia*. *Fucus serratus*, which in 1937 occurred on the wall only on the wet part near the out-fall, had, by 1939, spread to the drier parts also; while *Ascophyllum*, which has appeared since 1937, is generally though sparsely distributed. *Pelvetia* and lichens, however, do not yet seem to find suitable conditions on the wall. Finally, with the increased number of limpets there is a much larger area of wall browsed clear of algal felt. While the limpets are responsible for some mortality among the newly settled barnacles (Hatton, 1938, p. 338), there is a greater area available

for colonization, since barnacles cannot settle in a continuous felt. In general, then, the wall is probably approaching a climax.

The upper surfaces of the **stones** show little change in flora or fauna, except for some increase in the number of limpets on them, since 1937. The fauna under them has, however, increased considerably. Several species, including *Balanus perforatus*, *Porcellana longicornis*, *Gibbula umbilicalis* and probably several Amphipods, which were in 1937 restricted to the region near low water, had, by 1939, spread to the top of the beach. At the same time there has been an obvious increase in dampness under the stones, which is probably due to an accumulation of sand deep down among them; in places there are now standing pools at the foot of the wall. Weathering of the surface of the stones has probably made them more suitable for the settlement of some species, but the suggestion that the most important improvement in conditions lies in the increase in dampness is borne out by the fact that some of the species which have spread to the upper levels of the beach have been able to colonize the wall in those parts which are kept wet by seepage.

There is an accumulation of shingle in parts of the upper beach, but if sand also is present, it is not near the surface. Future changes in the fauna of the upper beach may therefore be expected to show a correlation with the extent to which such sand accumulates.

Near low water there has been a great increase in the substratum of **sandy gravel** in which many of the stones are embedded, and parallel with this is a considerable change in the fauna. Sponges and Ascidians, most of which have appeared since 1937, have almost covered the undersides of many of the stones with a resulting decrease in the numbers of the earlier colonizing *Pomatoceros*, *Spirorbis* and *Heteronomia*. At the same time certain free-living forms also have changed: *Pilumnus*, *Nassarius* and *Lagisca* having appeared since 1937, and *Porcellana longicornis* having become much commoner. *Porcellana platycheles*, on the other hand, seems to have decreased. Since the fauna at this level will be much less subject to desiccation than that at a higher level on the beach, it seems probable that the change that has made this habitat suitable for these recently arrived forms is the increase in mud, and that this factor is operative through their food requirements or feeding mechanisms. Assuming that the conditions on the old-established beach represent a climax, the similarity of the stones at low water on the new beach suggests that a similar stage has now been reached there.

Finally the **muddy gravel** under the low-water stones has begun to accumulate since 1937 only, and its fauna is probably still in a transitional state. In 1937 it contained numerous small Polychaetes mostly too young for specific identification, as well as the Ophiuroid *Amphipholis squamata*. The latter has decreased somewhat in abundance, but *Nereis pelagica* is fairly common, and *Arenicola grubei* present in small numbers, and all are well grown. Young *Paphia rhomboides* have appeared in small numbers.

In 1939 it was stated that "the general impression gained from two years' observation of the colonization of this piece of shore is definitely not one of keen competition for foothold among those species whose larvae are fortunate enough to settle before all available space is occupied, but rather of a very gradual occupation, with only some half dozen species capable of finding conditions suitable from the first. To the great majority of those species which were to be expected from comparison with a neighbouring old-established beach, conditions were obviously unsuitable at the commencement of observations, and for many they had not become suitable even after a lapse of two years".

By 1939 there were still a few species, such as *Pelvetia*, for which conditions seemed to be still unsuitable, and others, such as *Nucella* and anemones, which were rare because their means of dispersal does not allow a rapid spread. The intermediate levels of the shore (upper beach and lowest part of the wall) were still in a transitional state, but the upper and lower parts of the shore (upper wall and lower beach) appeared to have practically attained their climax conditions. With the influx of less tolerant forms permitted by the general improvement of conditions at these levels, the earlier phase of non-competition has given place to one with apparently a definite struggle for the available space, with a resulting change in the balance of the several species.

The fact that the highest and lowest zones of the new beach (upper wall and lower stony beach) have been colonized and have attained climax conditions at an earlier date than the intermediate zone (top of stony beach and lower wall) raises an interesting point in connexion with the general zonation and interplay of factors on beaches in general.

In the first place, the fauna and flora of the intertidal zone seem to fall mainly into two groups with their centres of distribution and optimum levels near high and low water respectively. Colman (1933), for example, has shown that on a rocky shore, there are more species present, and more with their upper and lower limits near high and low water than there are at mid-tide level. Elmhirst (1934) has shown a similar falling off in numbers of species with their centre of distribution near mid-tide, compared with those in the upper and lower zones of sandy beaches in general. Finally, Knight and Parke (1931) have described how certain algae which in summer occupy a wide vertical zone on the rocky shore, become restricted in winter to a much narrower zone, and how these algae fall into two groups, one of which is restricted in winter to a zone near high water, and the other to near low water.

There are, of course, some species which extend into the low-water zone but have their centre of distribution below water, but the low-water group as a whole is separated from the sublittoral groups by the fact that many of its species do not normally penetrate in any numbers below extreme low water. Similarly, in the intermediate mid-tide zone there are species which overlap this zone but have their centre of distribution above or below it, and some also

which actually have their centre of distribution there (e.g. *Cardium*: see Elmhirst, 1934), but these latter are fewer in number than those centring near high and low water.

Colman's observations on intertidal zonation show what may conveniently be termed a bimodal distribution: this seems to indicate less favourable general environmental conditions at mid-tide level than in the upper or lower zones. It may be that these conditions are brought about either by the individual factors being more favourable both above and below than at mid-tide level, or as the result of the interaction of several sets of factors, each with its optimum either at low or high water. It is probable that both are co-operative.

Among the factors which may tend to show an optimum near low water are desiccation, insolation and, in suspension feeders, duration of the feeding period. Those with a high water optimum include avoidance of lower-living enemies, and of the harmful effect of prolonged immersion as, for instance, the case of *Chthamalus stellatus* discussed by Moore & Kitching (1939, p. 526). It was found to occupy a restricted zone above and separated from that of *Balanus balanoides* which, therefore, does not limit the former by competition. Similarly, as pointed out by Moore (1935, p. 288), the high optimum zone of *B. balanoides* may be due to some inimical factor in the water, in addition to the favourable factor of higher wave exposure operative in this zone (Moore, 1935, pp. 283–5).

On the other hand, there are certain factors which seem to be more favourable at both high and low levels than at mid-tide level; these may well be associated with the fact that the rate of rise and fall of the tide is greatest at intermediate levels (Elmhirst, 1934). It is well known that a sudden small change may be more harmful to an animal than a gradual larger change. Any factor which has a different value for air and water, or which shows a stratification in the water, may be expected to subject the inhabitants of the mid-tide zone to a more rapid change than those living above or below. For example, Milne (1938) has shown that in the Tamar Estuary the rate of change of salinity is twice as great at mid-tide level as it is at low levels. Similarly, a change from sea to air temperature would take place most suddenly where the tide was falling fastest (allowing that the change of environment is never instantaneous, owing to splashing). Yet another effect is that mentioned by Elmhirst (1934); of the increase in current at mid-tide levels, making feeding (especially for those animals dependent on the ciliary current) more difficult there. Whatever the mechanism, then, the mid-tide environment seems generally to be less favourable than that above and below it.

Moore & Kitching (1939, p. 535) have proposed the general principle that departure from optimum conditions for one environmental factor may reduce the tolerance range of a species for a second factor.

Applying these two propositions to the new beach at Tinside, we find two groups of factors operative. First, the high- and low-water zones may be

expected to be more generally favourable to the species colonizing the beach than the intermediate zone, although the latter may not be outside their tolerance range under generally favourable conditions. Secondly, owing to lack of food, lack of moisture, unsuitability of an unweathered rock surface for the settlement of young, etc., the conditions on the beach as a whole in the early stages of its history will, irrespective of level, be less favourable than on an established beach. This second factor would reduce the tolerance range of the colonizing species, so that at first most of them would be able to colonize only the upper and lower levels. Later, with improvement of the general conditions (by various causes), they would be able also to spread to the mid-tide zone. A climax condition would, however, be reached first in the high and low water zones: which is what is observed on the new beach at Tinside.

4. Summary

The state of colonization of the flora and fauna on a new concrete wall and stony beach at Plymouth after six years is described, for comparison with a previous survey made during the first two years. Fourteen species of Algae and 71 species of animals were found. The highest and lowest zones of the beach appear to have developed more quickly towards a climax than the intermediate zone, in which environmental conditions are less favourable than in the others.

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OVIPOSITION IN GALL MIDGES (*CECIDOMYIDAE*) AFFECTING SEED PRODUCTION IN GRASSES[1]

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(*With* 1 *Figure in the Text*)

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1. Introduction and literature

The females of certain species of gall midges (Diptera, Cecidomyidae), the larvae of which live in the florets or seeds of grasses, oviposit on the flower-heads of the host plants only at certain times of the day. The oviposition thus exhibits a periodicity. It is, however, subject to modification by adverse weather conditions.

This periodicity in the oviposition has been noticed more particularly in the wheat blossom midges, *Contarinia tritici* (Kirby) and *Sitodiplosis mosellana* (Géh.). Kirby (1809) states that the females of *C. tritici* "were seldom to be seen much before 7 o'clock; at 8 the field appeared to swarm with them, at which hour they were all busily engaged in laying their eggs; and about 9 they generally disappeared". Fitch (1845), presumably referring to *S. mosellana*, writes: "In the twilight of evening it becomes active, and continues so perhaps through the entire night; for, before the morning sunrise it may be seen abundantly upon the wing." He also states that oviposition may occur to some extent on a cloudy day. Wagner (1866), referring to both wheat-blossom midges, confirms the statement of Fitch that oviposition continues all night, and claims to have seen isolated females up to 4 a.m. Ormerod (1890) notes that the females of *C. tritici* were busiest at the work (oviposition) about 8 o'clock in the evening. Kieffer (1900) agrees with Fitch that oviposition may

[1] Part of a dissertation submitted as partial fulfilment of the degree of Doctor of Philosophy in the University of Wales, 1937.

occur during the day if the sky is overcast. The most important contribution to our knowledge of the oviposition cycle in the wheat-blossom midges is that of Barnes (1932), who suggests that there is a partial correlation between the number of ovipositing females on the one hand and the direction and strength of the wind and the temperature of the soil and air on the other.

References to the oviposition of *C. merceri* Barnes are less numerous. Ormerod (1890), referring to what was almost certainly this species, writes: "Mr Edward Baillie...mentioned that on June 10th they were noticeable in great numbers *in the evening*, and again on June 26th, although at 5 a.m. he only secured two, yet in the evening they were plentiful." Barnes (1930) states that "oviposition takes place from 7.30 a.m. to noon, a pause around 1.30 p.m., going on again from 4.30 to 9 p.m. There is a crest of egg laying about 7.30 p.m. (all sun time)."

The only other grass-infesting species of *Contarinia* in which this egg-laying periodicity has been observed is an unnamed species on *Poa pratensis* L. and *P. trivialis* L. Tomaszewski (1931) states that the females of this species oviposit in the evening and night, if the weather is favourable; in windy or wet weather the midges take shelter at the base of the grasses.

Referring to *Dasyneura alopecuri* (Reuter), Barnes (1930) states that "there does not seem to be any marked crest of oviposition as in the case of *C. merceri*, for the females lay soon after emergence and go on all day". However, the same author records that this midge "was found swarming in large numbers on *Agropyronis repens* in July 1924", an observation which suggests that there may, after all, be variations in the intensity of oviposition.

This review of the literature serves to show that relatively little is known about the nature of the oviposition cycle and the extent to which it is affected by weather conditions. The subject is obviously of great importance to the seed grower, since, in all probability, the degree of infestation of the crop is largely dependent upon the type of weather prevailing during the flight period of the midges. Consideration of these facts led to the commencement of the present investigation in 1936. As the writer is no longer in a position to complete the investigation, it is considered advisable to place on record such information as is at present available.

2. Methods

Most of the observations recorded below were made upon *Contarinia merceri* Barnes infesting meadow foxtail (*Alopecurus pratensis*) on the Welsh Plant Breeding Station farm at Aberystwyth. It was the only species which was particularly abundant in the district. Furthermore, it was peculiarly suited to this type on investigation, owing to the fact that the inflorescences of meadow foxtail are compact and cylindrical and therefore easy to examine.

To obtain an estimate of the number of ovipositing females, 50 flower-heads

were examined at random *in situ*. The number of midges upon each was recorded, together with the times of commencement and completion of each count of 50 flower-heads. It was then possible to calculate a figure representing the average population of 100 flower-heads at the mid-period time. This figure may be termed the density of the population of ovipositing females. When observations had to be taken at night, artificial light was used, but during the interval between successive observations the light was extinguished so as to minimize interference with natural conditions.

Sunshine and wind records were kept at the farm meteorological station, which was situated close to the plot where most of the observations were made. Unfortunately, however, there were no records of hourly changes in soil and air temperature and air humidity.

3. Description of the oviposition cycle, with special reference to *Contarinia merceri*

In the case of *C. merceri*, if conditions are favourable oviposition begins in the afternoon, continues throughout the evening and night and ceases sometime during the following morning. If conditions are unfavourable, however, oviposition may be prevented for part of this period or even for the whole of it. The females ascend to the flower-heads either by crawling up the grass stems or by direct or indirect flight. Once on the flower-heads, they crawl very slowly from one floret to another, taking a considerable time to lay each egg. Then, sooner or later, they descend to ground level, where they take shelter among the stems and leaves of the grasses.

One complete oviposition cycle, as observed in *C. merceri* during June 1936, is represented graphically in Fig. 1. Migration up to the flower-heads began at about 5 p.m. and continued steadily until about 8 p.m. At the latter time, which was approximately half an hour before sunset, the density of the population of ovipositing females was at its maximum. Thereafter the downward migration set in and the population density fell to a low level at about 3 a.m. Shortly after 3 a.m. (about half an hour before sunrise) there was a sudden increase and after a few minor fluctuations the population density attained a second maximum, this time at about 6.50 a.m. Finally, some time after 7 a.m., there was a migration of females down to ground level until at 9.40 a.m. there was scarcely a single one left on the flower-heads.

Repeated observations showed that the evening oviposition maximum was attained frequently and with striking regularity. On those occasions when sufficiently accurate observations were made, it was found that this maximum occurred almost exactly half an hour before sunset. Moreover, oviposition (unless completely suppressed) always commenced at about 5 p.m., sometimes a little earlier but rarely later. The morning crest, however, was by no means as constant. On only three occasions was it found to have a maximum equalling that of the oviposition crest of the previous evening. On all other occasions it

was partly or completely obliterated. On those occasions when the morning crest could be observed the time of occurrence of the maximum varied from 6 a.m. to 8.30 a.m.

A significant occurrence in the oviposition cycle is the swarming or "dancing" which takes place at certain critical times. It was observed that this behaviour was most noticeable immediately before the maximum of the evening oviposition crest was attained. On the one occasion on which swarming was observed in the morning it accompanied or immediately preceded a slight increase in the number of females on the grass-heads; it also coincided with the first burst of activity on the part of Anthomyid flies. The significance of this

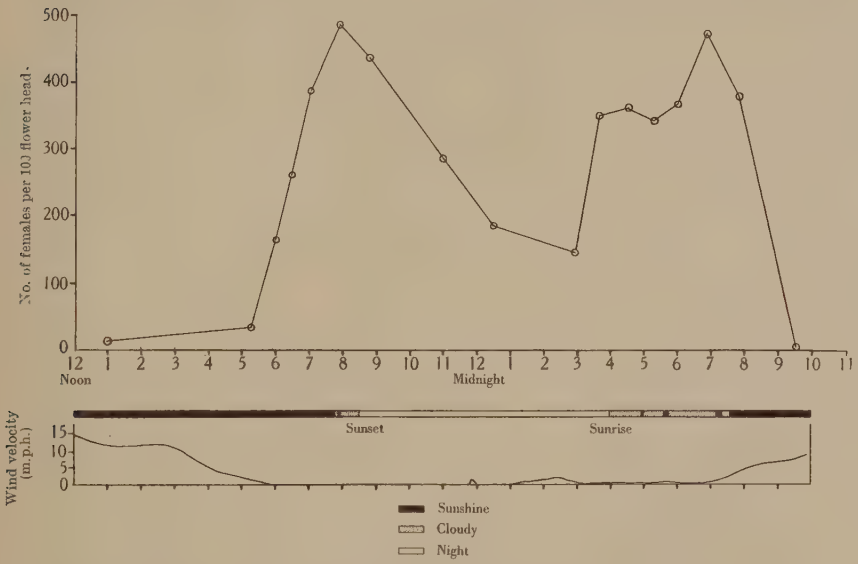

Fig. 1. One complete oviposition cycle of *Contarinia merceri* Barnes.

swarming is imperfectly understood. It takes the same form as the "courting flight" of certain other insects, but as far as the writer's observations go it is doubtful whether any males take part in it.

A similar oviposition cycle has been observed in *C. dactylidis* H.Lw., a species infesting cocksfoot grass (*Dactylis glomerata*). By making more or less simultaneous observations on *C. dactylidis* and *C. merceri*, it was found that fluctuations in the number of ovipositing females in one species were paralleled in the other species. During the period in which *C. dactylidis* was kept under observation, its morning oviposition crest appeared to be much less pronounced than its evening crest; but as, during the same period, *C. merceri* also had a relatively weak morning crest, it is probable that much the same relationship exists between the two crests in *C. dactylidis* as in *C. merceri*.

As there were no other species of grass gall midge sufficiently abundant in the Aberystwyth district, detailed observation was limited to these two species. On one occasion, however, the writer visited a certain district near Sarn, Montgomeryshire, where several other species of gall midges were known to occur in fair abundance. Observations were commenced at 6 p.m. and continued until 10 a.m. on the following day. It was found that there was quite a definite evening crest of oviposition in *C. lolii* Metcalfe on *Lolium perenne; Dasyneura dactylidis* Metcalfe on *Dactylis glomerata*; *Contarinia* sp. on *Holcus lanatus*; and *Sitodiplosis cambriensis* Jones, M. S. on *Poa pratensis* and *P. trivialis*. There was, however, no indication of a morning crest although, with the exception of *C. lolii*, oviposition continued until well after daybreak. The heavy morning mist may have been the cause of the absence of this crest.

As indicated in the review of the literature, a periodicity in the oviposition has been observed, in addition, in *C. tritici*, *Sitodiplosis mosellana* and the species of *Contarinia* found on *Poa pratensis* and *P. trivialis*. It would appear, therefore, that a single- or double-crested oviposition cycle is characteristic of most Cecidomyidae affecting seed production in grasses and cereals.

4. Some factors affecting the oviposition cycle

(*a*) *Light*

During the late afternoon and early evening, when the midges first begin to oviposit, they are to be found almost entirely on the shaded side of the flower-heads, i.e. the side directed away from the sun. Later in the evening the selection of the shaded side becomes much less pronounced and shortly after the oviposition crest has reached its maximum there may even be a selection of the sunny side. This suggests that oviposition is closely connected with variations in the intensity of light.

As stated above, the evening crest attained its maximum regularly about half an hour before sunset. It was noticeable that intermittent or light cloud during the evening had no apparent effect upon the oviposition crest. The occurrence of the morning maximum, however, seemed to be correlated with cloud conditions. Mist or cloud obscured the sun for a shorter or longer period every morning and the time of occurrence of the morning maximum and the subsequent cessation of oviposition were related in a general way to the time of effective appearance of the sun. Within a short time of this "effective dawn", oviposition had ceased and no more females could be found on the grass-heads.

The relation between the oviposition crests and the light intensity is illustrated in Fig. 1. It will be observed that (1) oviposition increases in intensity as the evening advances, continues, though not uniformly, throughout the night, and ceases some time after the effective appearance of the sun, and (2) that the two peaks of oviposition correspond with the transition

periods between day and night. It would appear that the relatively low intensity of oviposition during the early hours of the morning cannot be correlated with changes in light intensity. On this particular occasion there were intermittent periods of moonlight but it has not been possible on this or other occasions to demonstrate any connexion between oviposition and the appearance or non-appearance of the moon.

(*b*) *Wind*

The inability of the midges to cope with a wind of even moderate strength can be observed if the grass in an infested seed plot be disturbed so that the midges are made to rise into the air. Once they are deprived of the shelter normally provided by the foliage they are swept away. It is very noticeable, however, that the ovipositing females are by no means easily dislodged from the grass heads. It would appear, consequently, that the effect of air movement would be more apparent in the case of the upward migration. It would be less apparent once the midges were established on the flower-heads.

One particular series of observations showing the effect of wind on the number of ovipositing females was made on the night of 16–17 June, during a half gale. A very narrow zone along one side of the foxtail plot was sheltered by a neighbouring hedge. The occurrence of such a zone was evident from the fact that the grass heads in this region were comparatively still, whereas those in the rest of the plot were swaying vigorously. It was soon found that the heads in the sheltered zone were occupied by considerable numbers of ovipositing females, but there were very few females on the heads in the exposed part of the plot. It appears that there had been a more or less normal oviposition crest in the former position.

Observations made on a number of occasions showed that a wind velocity of more than about 10 m.p.h. (at a height of 50 ft.) completely inhibited oviposition on that part of the plot which was not sheltered by a hedgerow. Wind velocities of less than about 10 m.p.h. had little or no effect upon oviposition. It was estimated that the speed of flight of the females was roughly about human walking pace, i.e. 3 or 4 m.p.h. A breeze with a velocity of 5–10 m.p.h. at a height of 50 ft. would, it is surmised, have a velocity approximating to 3–6 m.p.h. at the height of the grass heads. This suggests that the important factor is the velocity of the air current in relation to that of the midge.

(*c*) *Flowering time of host grass*

It was noticeable that meadow foxtail flower-heads bearing exserted anthers were apparently much more attractive to the female midges than were those heads in other stages of reproductive development. For instance, on one occasion counts of females ovipositing on grass-heads with exserted anthers, and on grass-heads without exserted anthers, gave averages of 9·45 and 0·10

(S.E. ±0·73), the difference being clearly significant. On another occasion the averages were 14·50 and 0·59 (S.E. ±0·94).

The strong attraction exercised by the exserted anthers suggests that the time of flowering (i.e. time of day at which pollen is shed) may be a factor influencing the time of occurrence of oviposition. The weight of evidence, however, is against this supposition.

In the first place, the fact that at least a few midges alight and oviposit upon grass-heads not bearing exserted anthers is in itself an indication that pollen shedding is not the sole determinant. In the second place, the time of flowering in meadow foxtail is between 6 and 11 a.m. (Beddows, 1931), whereas the main, and often the only, oviposition crest for *Contarinia merceri* occurs in the evening at about 8 o'clock.

With regard to species other than *C. merceri*, the writer has not made any extensive observations but, in the case of *C. dactylidis* at least, casual observations in 1935 and 1936 appear to suggest that there is no selection of heads with exserted anthers. Furthermore, among grasses in general there is considerable variation in the time of flowering (Beddows, 1931), but the results of the present investigation lead to the conclusion that the oviposition cycle described for *C. merceri* is more or less characteristic of most species of *Contarinia* affecting seed production in Pooid grasses. This lack of correspondence between the time of flowering and the oviposition crest of the particular midge pest provides sufficient reason for concluding that the shedding of the pollen is a relatively unimportant factor.

(*d*) *Other factors*

Among other factors which may influence the periodic oviposition of these midges is the time of emergence from the pupal stage. In *C. merceri* (Barnes, 1930) the crest of emergence of the males occurs just before noon and that of the females just after. It would appear, therefore, that there is no correspondence between the single emergence crest of the females and the double oviposition crest.

5. Summary

In certain species of gall midges (Cecidomyidae) affecting seed production in grasses, in particular *Contarinia merceri* on *Alopecurus pratensis*, oviposition exhibits a diurnal periodicity. In favourable weather, oviposition occurs mainly between 5 p.m. and 8 a.m. (G.M.T.), with a crest shortly before sunset and another sometime after sunrise. Oviposition is very much influenced by the intensity of the light and the velocity of the wind. Contrary to expectations, the time of flowering of the host grass appears to have no relation to the time of oviposition.

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REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 28, No. 2, August 1940)

This number contains 11 original papers dealing with problems of vegetation and ecology, an obituary notice, two reviews and numerous notices of papers. The first papers, contributed by R. Scott Russell and his associates, are the second and third parts of physiological and ecological studies on an Arctic vegetation (Jan Mayen Island), dealing firstly with the development of soil nitrogen supply and soil micro-organisms (bacteria and protozoa) and, secondly, with carbon assimilation, carbohydrate storage and stomatal movement in relation to plant growth. E. J. Salisbury and F. W. Jane follow with an account of charcoals from Maiden Castle and their significance in relation to the vegetation and climatic conditions in prehistoric times.

Three of the papers deal with grazing effects on British grasslands. The results of varying grazing and manurial treatments on natural hill pastures are described by W. E. J. Milton. These are detailed results from the well-known experiments of the Welsh Plant Breeding Station, in progress since 1930. In an article on chalk grassland successions from arable areas and quarry spoil banks, J. F. Hope Simpson describes changes in the last sixteen years and stresses the importance of grazing in determining the final character. In another paper E. Wyllie Fenton gives examples of the influence of rabbits on certain hill pastures in Southern Scotland. The grasslands of Kenya (and other vegetation types) are mapped and described by D. C. Edwards. Another paper on overseas vegetation by D. Vesey-Fitzgerald deals with the vegetation of Seychelles with particular reference to the fast vanishing forests of the islands; while R. F. Jones describes the plant ecology of Lake Huleh, in Palestine, and its surroundings, particularly a large Papyrus swamp.

Only two papers deal with maritime ecology. T. K. Rees gives a detailed analysis of algal colonization at Mumbles Head, S. Wales, from observations extending over three years; while J. M. Lambert and M. R. Davies describe the colonization by plants of a sandy area in the Dovey Estuary. The articles are completed by an appreciation of the late H. C. Cowles by A. G. Tansley. There is a list of papers dealing with freshwater algal ecology (published since 1930) by E. M. Lind. The number is concluded by two reviews, one of the *Journal of Animal Ecology*.

W. H. PEARSALL.

A STOCKTAKING OF WILDFOWL

John Berry (1939). *The status and distribution of wild geese and wild duck in Scotland.* International Wildfowl Enquiry: Vol. 2, 190 pp., 5 photographs and a map. Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Price 10*s.* 6*d.*

For several years the attention of a special Subcommittee of the British Section, International Committee for Bird Preservation, has been concentrated on an inquiry into the present status of wild ducks and geese in the British Isles. This book represents Volume 2 of this investigation. (At the time of writing this review Volume 1 has not appeared.)

One is always inclined to take a gloomy view of the reduction in numbers of ducks and geese, but Dr Berry shows that though the introduction of breech-loading guns, mechanical transport, drainage and so on began, apparently almost immediately, to reduce the numbers of wildfowl more or less all over the world, various protective measures are helping to check this decline in numbers and, as regards Scotland, at any rate in comparatively recent times, the situation is much more comforting than one has been led to believe.

As to the geese he says: "Taken collectively, the total numbers of Wildgeese now wintering in Scotland appear to show an increase over the past fifty years but a decrease over the last five." Again: "The Black Geese—Brent and Barnacle—appear to have been becoming gradually less abundant over a very long period of years. On the other hand, Western Bean is the only species or race of Grey Goose which seems to have become less plentiful during the last hundred years. All the others—Greylag, White-fronted, Yellow-billed Bean, and above all Pinkfoot—have shown a very definite increase over the past fifty years."

Eight species of surface-feeding ducks are given. In the breeding season probably six are increasing, none decreasing and two show no change. In winter probably five are increasing, two decreasing and one no change. Ten species of diving-ducks are given. With the regular breeders probably four are increasing, none decreasing and the rare breeders show no significant change. With the three sawbills the two breeding species are increasing and, in the winter, two if not all three are increasing.

These reports on abundance are presented in admirably full detail, each species having a separate discussion under each faunal area. Other than these there is much to interest the ecologist. Enemies, for example, are discussed under such categories as gulls, swans (which monopolize ponds for nesting), rats, stoats, etc., angler fish and pike, and man with his manifold influences including oil pollution, netting, egg-taking, draining, afforestation and shooting. As to the latter, the author considers the disturbance more important than the actual numbers killed and gives interesting examples of the more adaptive species changing their habitat or behaviour to escape it. Damage to arable land by geese is considered to outweigh the good, but they are decidedly beneficial to pasture—mostly showing a preference for such undesirable weeds as *Ranunculus* (including the roots) to grass.

Temperature statistics over the periods 1871–1900 and 1906–35 show that the Scottish winters are becoming milder. This would no doubt contribute towards an increase in wintering species.

The ecologist will like also the pictures presented of fluctuating numbers, of sudden spurts, and of colonizations (as with that of the goosander, p. 148). Eighteen references are given, a map of the faunal areas of Scotland and a detailed index. Two of the plates show examples of Dr Berry's effective method of counting large flocks of geese, either on the ground or in flight, by means of a "panorama" on a cine-camera. L. S. V. VENABLES.

TWO GREAT MARINE ECOLOGICAL SURVEYS

(1) (*a*) **T. A. Stephenson, Anne Stephenson & C. A. Du Toit (1937).** "The South African intertidal zone and its relation to ocean currents. I. A temperate Indian Ocean shore." Trans. Roy. Soc. South Africa, 24: 341–82.

(*b*) **N. A. H. Bokenham, F. L. M. Neugebauer & T. A. Stephenson (1938).** "The vertical distribution of certain intertidal marine Gastropods in False Bay...." Ann. Natal Museum, 9: 113–37.

(*c*) **T. A. Stephenson (1939).** "The constitution of the intertidal fauna and flora of South Africa. Part I." J. Linn. Soc. (Zoöl.), 40: 487–536.

Cape Town University, where this work is being done, lies near the meeting place of two ocean currents with very different temperatures. The Moçambique current flowing southwards down the east coast of Africa, and known in its further extension as the Agulhas current, brings warm water to meet an upwelling of much colder water which impinges on the south-west coast and is known as the Antarctic intermediate water. This upwelling appears near the coast, but the ocean is warm again farther out. In many respects, both physical and ecological, this upwelling water reminds us of the similar phenomenon off the west coast of South America: formerly known as the Humboldt current, but now called the Peru coastal current. The sea water on opposite sides of the narrow peninsula at Cape Town may show a

difference in temperature of as much as 8° C. on the same day. Here is a fascinating ecosystem for survey, and comparison with other parts of the world.

Since 1932 Prof. Stephenson has organized a large amount of ecological collecting and mapping, the results of which are now available. These results represent the necessary first stage of general observation and tabulation of species, zones, distribution in relation to temperature and so on. They are not simply catalogues of plants and animals, but compact community surveys partly done by quantitative methods, and spaced out in a chain of collecting stations along a stretch of African coast sufficiently large to have satisfied Humboldt himself.

I have selected for review the three more general papers, but these are amplified in detailed reports by various workers in the *Trans. Roy. Soc. S. Afr.* (1938), 26: 49–88; and the *Ann. Natal Mus.* (1938) 9: 1–111 and (1939) 9: 283–306. The first and third of the papers reviewed here cover somewhat the same general ground, the third begins a more intensive analysis of the zonation problem.

There are not many surveys yet which give such a complete picture of the life between tide marks, and very few which describe the complete community. At Still Bay and neighbouring points, as an example of the intertidal community of a fairly warm temperate region, there were 46 species of Algae and at least 246 of animals. The animals included: Foraminifera, 1; Porifera (sponges), 29; Coelenterata (hydroids etc.), 15; Turbellaria (flatworms), 6; Nemertine worms, 1; Polychaete worms, 27; Gephyrean worms (not identified); Polyzoa (moss animalcules) 10; Brachiopoda, 1; Crustacea, 45; Arachnida, 2 (including one Pycnogonid and one spider); Insects, 1; Mollusca, 69; Echinodermata (sea-urchins, starfish etc.) 17; Ascidiacea (sea-squirts) 15; fish, 7 (all in pools). The photographs accompanying all these reports are magnificent and vividly ecological.

Two chief problems (apart from the large ones involved in organizing surveys on this scale and maintaining the enthusiasm and standards of work of a changing group of students) that have received attention are (1) the changing character of communities along the temperature gradient between the almost coral reef community at the limits of their eastern stations and the more temperate conditions on the south-west, (2) the nature and limits of intertidal zones. The discussion built up about these problems cannot be reviewed in detail here; but the authors appear to have satisfied themselves that the very striking zonation of certain abundant species (the lower *Cochlear* (limpet), intermediate *Balanoid* (barnacle) and upper *Littorina* (gastropod)) are more than merely convenient indicators of the limits reached by three abundant forms. However, one would like to have a rather more clear distinction drawn between "dominant" animals used for the convenience of making surveys of habitat zones, and the implication that there are actually quite distinct animal communities showing (among the other species as well) abrupt changes at the same lines on the shore as the dominant species. We have here a similar problem to that met with in vertical plant zonation, e.g. on mountains. How far do the limits marked by the abundant and conspicuous forms correspond to or control the general limits of the communities as a whole? Do such general limits exist?

There are interesting discussions also of the differences between these South African communities and intertidal communities elsewhere. The absence or rarity of a Laminarian zone on many parts of the coast examined is mentioned as one of the important differences. It is much to be hoped that this survey will continue and become more analytical as it progresses. It ranks as one of the major ecological ventures of this century.

(2) (*a*) **A. C. Hardy (1939).** "Ecological investigations with the continuous plankton recorder: object, plan and methods." Hull Bulletins of Marine Ecology, 1, No. 1: 1–57. Price 5*s*.

(*b*) **Anon. (1939).** "Ecological investigations with the continuous plankton recorder: summary list of records, 1932–37." Hull Bulletins of Marine Ecology, 1, No. 2: 59–71. Price 1*s*.

(*c*) **C. E. Lucas (1940).** "Ecological investigations with the continuous plankton recorder: the phytoplankton in the southern North Sea, 1932–37." Hull Bulletins of Marine Ecology, 1, No. 3: 73–170. Price 12*s*. (Copies of these may be purchased through the Registrar, University College, Hull.)

Hardy's genius for ecological gadgets is well known to his friends, and partly also to the scientific public who have already seen accounts of his plankton recorder and of the methods of collecting "aerial plankton" by means of kite nets.

The establishment of a Department of Zoology and Oceanography in University College, Hull, has given him the opportunity of starting organized plankton transects across the North Sea, by providing ordinary ships with continuous plankton recorders which they tow back and forth on their journeys. The actual designing of the machinery, which is fully described in the first report; the diplomacy and organization required to get regular assistance from shipping companies; and the training of a laboratory staff in new counting techniques with the material obtained, in themselves represent a triumph in ecological research organization. We are now able, from this series of new reports, to judge how successful the system has been and is likely to be in giving measurements of plankton conditions across standard transects from year to year.

So far only the phytoplankton has been published, but we are promised a next number dealing with Copepoda. The war has of course completely brought field work to a standstill, but the time has been profitably used in analysing and presenting the results. The treatment is clear and very full, with particularly good maps and diagrams, which enable one to see the quantitative data superimposed on actual maps of the transects. No. 1 frankly considers the various advantages and disadvantages of the sampling system which the continuous roll of gauze in the recorder collects, as the apparatus is towed along (so far using still a constant depth, though a new modification may enable it to make a swallow-like progress under water, and so overcome some of the sampling difficulties caused by vertical migration of the plankton etc.). It is concluded that the picture obtained is substantially correct, and that it in any case enables comparisons of abundance from year to year to be made. The patchiness of plankton in the water is again found to be a very important feature.

In No. 3 special analysis has been made of two diatoms (*Rhizosolenia styliformis* and *Biddulphia sinensis*), of *Phaeocystis* and of the Dinoflagelates as a group (and species of *Ceratium* in particular). The first three of these are important in herring ecology. With five and a half years' material, collected throughout the year, we get a magnificent picture of the problem in its full scale—fluctuations in abundance and in position of maximum abundance from month to month and year to year, but with certain seasonal and long-term trends standing out. The figures enable correlations to be made between the occurrence of different species and so to express some of the elements of marine community life in quantitative terms. There is, for instance, the general tendency for the two diatoms mentioned above to have their maximum incidence at different times, although these times vary from year to year in both species. There is also a negative correlation between them and *Phaeocystis*, and between *Phaeocystis* and Dinoflagellates. During the period of the survey up to 1937 there was on the whole an increase in abundance of all the forms on these transects, though within that trend there were several marked fluctuations. Such data are being gradually woven into a general fabric of knowledge about the movements of fish and their ecological background, and we shall look forward to a revival of this transect work when the war is over, and its establishment as a feature of marine ecology as permanent as meteorology or tidal observations.

CHARLES ELTON.

COLOURS OF ANIMALS

Hugh B. Cott (1940). *Adaptive coloration in animals.* xxxii + 508 pp., 49 plates and 84 text-figures. Methuen & Co. Ltd., 36 Essex Street, Strand, London, W.C. 2. Price £2.

Animal coloration and its adaptive significance has been a bone of fierce contention amongst evolutionary protagonists for a hundred years. Periodically attempts have been made to sum up the state of knowledge into a single book. Sir Edward Poulton's *The colours of animals* was the pioneer work in this field. Dr Cott's book is a much needed and worthy successor to it.

Dr Cott is described in the introduction as a true follower of Darwin who drives his conclusions home by sheer weight of examples, and it is at this level that the book will find its greatest value. More than two-thirds is devoted to a careful analysis of effacement and advertisement, excellently illustrated with photographs and with drawings from the author's own pen. Although there is some discussion in the first pages on the effects of different spectral structure on the nature of the image produced, most of the argument is given on the assumption that the image that can be produced by the camera or by art from the memory of the image received by the human eye is very like that produced in the eye of the predator, whatever it may be. This apparent fallacy has always been one of the most powerful arguments of the opponents of adaptive coloration. Dr Cott, being a firm believer of the truth contained in his title, gives 100 pages of detailed analysis of the methods by which concealment is attained before defeating this and other opposition arguments. It is a pity that only 40 pages should have been devoted to this end, leaving perhaps a loophole for antagonists to continue arguments that should have been completed once and for all.

For the very reason that this book is an analysis of the physical, rather than the physiological and genetic, mechanism by which adaptive coloration is attained, certain sections which have received disproportionate attention in the past have been relegated to a more balanced position. Thus mimicry, which is only a small section of special resemblance to particular objects, is dealt with in 17 pages. The optical effects produced by mimics are the same as those produced by models, which are fully dealt with under the heading of "the appearance and behaviour of aposematic animals".

The reviewer of this book in *Nature* has already argued at length its great value as a manual of camouflage technique. At that time the detailed knowledge of animal camouflage possessed by ecologists was being misused or entirely neglected by those responsible for protecting the men and machines of war. It is hoped that a satisfactory combination of scientist, artist and soldier has now been set up which will rectify the earlier inefficiencies. This book is no arm-chair nature study but has, both in the text and in the illustrations, innumerable examples and rules of immediate practical application.

The general make up and editing of this book are excellent; it is readable without being chatty and scientific without being pedantic. Three suggestions for future editions may be made. Although authorities for scientific names of vertebrates can often be dispensed with, names of insects lose much of their value without them. Invalid names, even when checklists are easily available, are very common. The bibliography, of about 700 items, contains few mistakes or misprints, but suffers from a great lack of uniformity, particularly in the abbreviations used for periodicals.

R. B. FREEMAN.

SHORT REVIEWS

Zoology of Cambridgeshire, edited by **A. D. Imms** in *The Victoria County History of Cambridgeshire and the Isle of Ely*, 1: 77–245, edited by **L. F. Salzman**. 1938. Oxford.

Zoology of Oxfordshire, edited by **B. M. Hobby** in *The Victoria County History of Oxfordshire*, 1: 57–222, edited by **L. F. Salzman**. 1939. London.

Faunae lists whose limits are governed by political rather than physical geography suffer from many disadvantages, and these two volumes, although they should, being sponsored by the zoological departments of Oxford and Cambridge Universities, be models of their kind, are no exception. Boundaries of convenience, such as the Thames in Oxfordshire, divide areas which are not only well-recognized collecting grounds, but geological and faunistic entities which cannot be satisfactorily treated apart.

Lack of uniformity, such as the absence of Turbellaria and Hirudinea from the Oxfordshire volume or of many insect orders (particularly the Hemiptera-Homoptera and Siphonaptera) from the Cambridgeshire; and omissions such as no mention of Protozoa or Coelenterata in either volume, which might easily be remedied, decrease the value of these works. Lack of uniformity within the volumes is also too common; in many places full locality data and habitat notes are given while in others there is nothing but a list.

Over this adverse criticism these volumes have a very real value as basic working data, gathering together records from local and often obscure sources, and small ecological notes which would not otherwise be published. In both volumes the editing has been most carefully done, giving them an additional value as check-lists. R. B. FREEMAN.

British Trust for Ornithology (1940). Publications, Vol. 1 (1935–9). Obtainable from The Director, Edward Grey Institute of Field Ornithology, 39 Museum Road, Oxford. Price 6*s*.

The first thing that strikes a reader glancing at this volume is the large proportion of papers that deal with census taking. Ten of them (including five devoted only to herons) have as their object the estimation of actual numbers, while two more deal with habitat preferences and distribution of certain species, naturally involving a number of counts. It is both a striking development in ornithology generally and a justification of such an organization as the British Trust, that co-operative census taking is so widespread now. In Great Britain, if in any country, taxonomic problems should have come to an initial equilibrium sufficient to enable quantitative problems to be tackled.

The easiest problems have been approached first, and these papers may be regarded as feelers, exploring methods and pointing the way to more exhaustive investigations. Heathland breeding populations and heron and grebe censuses are of this type. Other papers deal with more general biological problems, food analyses, migration, dimorphism, etc. On the whole this represents a considerable mass of information resulting from the first five years of the Trust's existence, and one can only hope that such a promising beginning will be maintained.

When this volume has been produced at such a moderate price, it may seem unfair to cavil at the format. The fact remains, however, that the cutting down of the larger papers and the folding of the plates is very unsatisfactory and it is to be hoped that subsequent volumes will overcome this drawback. H. N. SOUTHERN.

H. H. Bennett (1939). *Soil conservation.* 994 pp., 358 text-figures and photographs, 17 maps. McGraw-Hill Publishing Co. Ltd., Aldwych House, London, W.C. 2. Price £2.

An important and detailed account of the damage done to American agriculture by exposing the top-soils and removing natural vegetation; of the gradual realization of the situation; and of the building up since 1933 of the Soil Erosion Service. About 13,000 million

acres are already damaged, wholly or partly, and the annual loss of solid material from the land is put at 3000 million tons. The Soil Erosion Service is working successfully by propaganda, by demonstrations, and by arranging schemes of erosion control for farmers to put into practice. All aspects of erosion control are treated and a valuable survey of the main farming areas of the United States is given. H. N. SOUTHERN.

H. Eliot Howard (1940). *A waterhen's worlds.* Large octavo, 84 pp., 2 plates. Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Price 10*s.* 6*d.*

The chief interest of this book for an ecologist lies in the careful analysis of a bird's interrelations with its environment, both external and internal. The latter is especially carefully dealt with. We are only too apt to think of any animal as being a passive machine hedged about by innumerable forces against which it keeps impinging; this is chiefly because it is much more difficult to envisage the reciprocal effect of the organism on its environment. The nature of the surroundings, as they exist for the bird, can only be painfully adumbrated after tireless watching and careful analysis of its activities.

The actions of a pair of waterhens, who had a territory in and about a pond near the author's house, are described with minuteness and clarity throughout the major phases of the breeding season. The main pre-occupation is with the connexion between actions and feelings, the different worlds depending on the bird's own state, which form the background of such feelings, and the bird's capacity for perceiving these worlds from sensual and mental data. Facts of importance for the ecologist which emerge are the importance of the emotional bond existing between a pair of birds (see especially the chapter on "Platform World"), the disjoining of this from the sexual world and the extraordinarily interesting reactions to absence of mate and to trespassing.

It is perhaps unfortunate that some physiological data have been imported without full realization of their implications. The endocrine balance and its relation to metabolism are so ill-understood and seem so complicated as yet, that it is useless to expect any but the broadest trends of behaviour to conform with changes in this balance.

Apart from this the book is a worthy successor to the previous ones, which have made the author so deservedly well known.

H. N. SOUTHERN.

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copies of these notices are no longer issued free with the *Journal*, but they can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s*. 6*d*. per annum post free (normally about 300 notices, in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, C. Elton, R. B. Freeman, B. M. Hobby, M. Mare, Barrington Moore, E. Nelmes, F. T. K. Pentelow, H. N. Southern, H. G. Vevers and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO THEIR HABITAT

(*a*) Marine and brackish

Hartley, P. H. T. (1940). "The Saltash tuck-net fishery and the ecology of some estuarine fishes." J. Mar. Biol. Ass. U.K. 24: 1–68.

An analysis of samples taken over a period of two years with the Saltash tuck-net which is used for seining over mud in the Tamar and Lynher rivers. The fauna is essentially marine. Growth rates and food are worked out for a number of fish, particularly the flounder (*Pleuronectes flesus*).

Milne, A. (1940). "The ecology of the Tamar estuary. IV. The distribution of the fauna and flora on buoys." J. Mar. Biol. Ass. U.K. 24: 69–87.

Details of the horizontal and vertical distribution of the macro-fauna and macro-flora of buoys situated from the mouth of the estuary to the open sea. Since buoys move up with the tide the exposure factor is eliminated and salinity becomes the most important.

Nichol, E. A. T. (1938). "The brackish-water lochs of Orkney." Proc. Roy. Soc. Edinb. 58: 181–91.

Lochs Stenness and Harray on the mainland are the only brackish lochs in the Orkneys; they are the only known Scottish stations for *Neritina fluviatilis*. The macroscopic fauna is enumerated; it is composed of forms typically from fresh and salt water.

Rees, C. B. (1939). "Notes on the ecology of the sandy beaches of north Donegal." Proc. R. Irish Acad. 45, B: 215—29.

A study of the macro-fauna of beaches in its relation to various physical factors, particularly tide-exposure, salinity and texture of sands.

Colman, J. (1940). "On the faunas inhabiting intertidal seaweeds." J. Mar. Biol. Ass. U.K. 24: 129–83.

An analysis of 177 species of invertebrates in association with eight seaweeds on Church reef, Wembury.

Kevan, D. K. (1939). "Further notes on *Limapontia depressa* (A. & H.) var. *pellucida* Kevan." J. Conch. 21: 160–2.

It is probable that the breeding of this Nudibranch takes place in the brackish waters where the adults are usually found, but that the veliger stage develops in sea water.

Moore, H. B. (1940). "The biology of *Littorina littorea*. Part II. Zonation in relation to other Gastropods on stony and muddy shores." J. Mar. Biol. Ass. U.K. 24: 227–37.

Medium-sized individuals occur throughout the vertical range; large ones are densest at the bottom and small ones at the top.

McMillan, N. F. (1939). "*Littorina saxatilis nigrolineata* Gray." J. Conch. 21: 173–4.

Occurs in north Wales, Anglesey and Barra, Outer Hebrides, but not in Ireland.

Purchon, R. D. (1939). "The effect of the environment upon the shell of *Cardium edule*." Proc. Malacol. Soc. 23: 256–67.

It is shown that shells from estuarine mud are more lightly built, possess fewer ribs, and are more symmetrical than those from marine, wave-beaten, sand. This measure of asymmetry increases logarithmically with age and the greatest rate of increase and the highest measures of asymmetry are found in estuarine samples.

Williams, G. E. (1939). "Severe mortality of *Mactra corallina cinerea* (Montagu) off the Lancashire coast." Nature, Lond. 144: 1049.

In October 1939 about 600,000,000 of the lamellibranc *Mactra corallina cinerea*, all of the same year's spat, were washed up on the Lancashire coast, during spring tides with an offshore wind, forming a continuous belt 9 miles long, 6 ft. wide and 10 in. deep. By 1 November, most were dead and the belt had been broken up by the tide into five drifts parallel with the high-water mark, the shoreward drift being the heaviest, and extending over a zone averaging 25 yd. in width. Similar phenomena in which three other species were concerned occurred in 1891 and 1929; changes in the fauna of the sea-bed during intervening years, or action on different parts of the bed, may have caused different species to be affected on each occasion.

Orton, J. H. (1940). "Effect of the severe frost of the winter of 1939–40 on the fauna of the Essex oyster beds." Nature, Lond. 145: 708–9.

The entire stock of Brittany oysters and 42–69% of the native oysters on the beds in the Rivers Blackwater and Roach were destroyed during severe weather at the beginning of 1940 when the temperature of the Blackwater remained about 0° C. from 1 January until 19 February, and ice-floes persisted for a month. The causes of mortality are briefly discussed; it was greatest in shallow and enclosed waters, and among large and relaid oysters. *Crepidula fornicata* was weakened, but a chain brought into warmer conditions on 1 March recovered to some extent by 7 March. Other bottom-living forms did not appear to be affected, but no specimens of *Purpura* or *Ocinebra* were obtained.

Cole, H. A. (1940). "Effect of the severe winter of 1939–40 on British oyster beds." Nature, Lond. 145: 976.

A survey made during April 1940 established that practically the entire stock of Brittany oysters (*Ostrea edulis*) on Essex and Kent beds was destroyed during severe winter weather, whereas losses in Devon and Cornwall were comparatively slight. Losses of native oysters varied from about 50 to 80% in Essex, but are not expected to reach 50% in Kent, and were slight in Cornwall. Mortality among American and Portuguese oysters (*O. virginica* and *O. angulata*) in Essex varied from 25 to 50%. Tank-bred oysters in north Wales and south Devon were only slightly affected, and no losses were observed among slipper limpets (*Crepidula fornicata*) except in the River Medway; or among *Urosalpinx cinerea*, which appears to have replaced *Ocinebra* on the Essex coast.

Panikkar, N. K. (1940). "Osmotic properties of the common prawn." Nature, Lond. 145: 108.

Leander serratus, an essentially marine littoral species of prawn, shows osmotic behaviour unusual in a marine invertebrate. Its ability to maintain the osmotic pressure of the blood near the optimum is not well developed: there is a steady decline in dilutions of salt water below 2·5% sodium chloride. It may have taken secondarily to marine life.

Frost, W. E. (1939). "Larval stages of the Euphausiid *Thysanopoda acutifrons* (Holt & Tattersall) taken off the south-west coast of Ireland." Proc. R. Irish Acad. 45, B: 301–19.

Oceanic species of Euphausiids appear to have stabilized the furcilia development (i.e. successive moults show certain definite degrees of development) more than the neritic species have done. They have more nearly achieved metamorphosis.

Goodhart, C. B. & Harrison, R. (1940). "Occurrence of some off-shore Amphipods in the littoral zone." Nature, Lond. 145: 109.

Four species of amphipods (near Drumberg, Sutherland) are reported from the intertidal zone for the first time: *Ampelisca spinimana*, *Harpinia antennaria*, *Leucothöe spinicarpa*, *Phtisica marina*.

(*b*) Fresh water

van Someren, V. D. (1940). "The factors conditioning the rising of trout (*Salmo trutta*) in a small fresh-water lake." J. Anim. Ecol. 9: 89–107.

Rising of trout in a small lake in Surrey is correlated with water temperature of the preceding 24 hr. more than with other factors, high temperatures being unfavourable. The evening rise commences always the same length of time after sundown, 20–30 min., and lasts about 30 min. Light and the hatch of "fly" are also important limiting factors.

Macan, T. T. (1940). "Dytiscidae and Haliplidae (Col.) in the Lake District." Trans. Soc. Brit. Ent. 7: 1–20.

Tabulates 11 species of Haliplidae and 25 Dytiscidae, indicating their relative abundance in different habitats. None of the species appears to be restricted to a narrow range of habitat requirements.

Reid, D. M. (1939). "On the occurrence of *Gammarus duebeni* (Lillj.) (Crustacea, Amphipoda) in Ireland." Proc. R. Irish Acad. 45, B: 207–14.

G. duebeni is the fresh-water species in Ireland, whilst in England this species only occurs in brackish water, being replaced by *G. pulex* in fresh water. Brackish water *G. duebeni* can live, but not breed, in fresh water, indicating some physiological difference. It is suggested that the two races should be designated α (fresh) and β (brackish).

Pocock, M. A. (1938). "*Volvox*-hunting in Gloucestershire ponds." Proc. Cotteswold Nat. Fld Cl. 26: 318–22.

Notes on the habitats of three species of *Volvox* and other Protozoa.

(*c*) Land

Lack, D. (1939). "The behaviour of the robin. Part I. The life-history, with special reference to aggressive behaviour, sexual behaviour, and territory. Part II. A partial analysis of aggressive and recognitional behaviour." Proc. Zool. Soc. Lond. A, 109: 169–219.

An important investigation, by means of colour ringing, of the relationships existing in a population of robins. Posturing and aggressive behaviour, including the use of the red breast as a "threat colour", are shown to be territorial and not sexual. Occupation of territory, pair formation, which occurs in December long before breeding, sexual behaviour, etc., are described. Autumn territory may be due to a recrudescence of spring physiological conditions. Aggressive behaviour is shown to depend on a complex of stimuli, internal and external, including shape, movement, song, and redness. Stuffed birds are attacked by owners of territory under certain conditions, and even a patch of red breast feathers may suffer similarly.

Lack, D. (1940). "The releaser concept in bird behaviour." Nature, Lond. 145: 107–8.

Recent work on aggressive behaviour in the British robin (*Erithacus rubecula melophilus*) which demonstrated a tendency towards incomplete separation into three main reactions, each with its own releaser, suggests that, at least in this case the explanation of bird behaviour provided by the releaser concept should be modified. In general, releasers are considered to be secondary and not fundamental units of bird behaviour, which is originally a response to a general situation. Later in the history of the species or of the individual, one part of the external environment tends to become of primary importance, and may then appear to evoke the whole response, which, however, may also be induced by other stimuli. Colour pattern is an important factor in this respect. The physiological state of the bird must also be considered.

Edelsten, H. M. (1940). "The insect fauna of the waste areas of Tilbury Dock." Proc. R. Ent. Soc. Lond. A, 15: 1–11.

271 species are recorded: 15 butterflies, 183 moths, 46 beetles, 13 bugs, 8 Hymenoptera and 6 Diptera.

Fisher, R. C. & Tasker, H. S. (1940). "The detection of wood-boring insects by means of X-rays." Ann. Appl. Biol. 27: 92–100.

A valuable method of detection and study.

Mellanby, K. (1939). "Low temperature and insect activity." Proc. Roy. Soc. B, 127: 473–87.

The temperature at which an insect is immobilized by cold is determined by the temperature at which the animal has been previously kept. Thus the chill-coma temperature of a cockroach which has lived at 14–17° C. is 2·0° C.; after exposure to 36° C. it is 9·5° C. Recovery from the chill-coma temperature is rapid, from lower temperatures it is slow. The cold-death point is also dependent on the previous temperature history. Rate of movement of the bed bug varied from 59 cm./min. at 15° C. to 255 cm./min. at 32° C.

Lisney, A. A. (1940). "New records for Irish Lepidoptera." Entomologist, 73: 123–8, 150–5.

A useful supplement to the records contained in Donovan's *Catalogue of the Macrolepidoptera of Ireland.*

Bretherton, R. F. (1940). "A list of the Macro-Lepidoptera of the Oxford district." Proc. Ashmol. Nat. Hist. Soc. 1939: 25–70.

62% (515 out of 828) of the British species occur within 10 miles of Oxford.

Wilson, G. Fox- (1940). "Phenological observations on the brimstone butterfly, *Gonepteryx rhamni* (Linn.) (Lepid.)." Proc. R. Ent. Soc. Lond. A, 15: 13–16.

Give records over a period of 20 years (1920–39) which are correlated with maximum and minimum temperatures and hours of sunshine for a period of 7 days prior to emergence from hibernation. Humidity and rainfall were found to show no effect on the awakening process.

Hill, A. R. (1940). "A brief review of the Acrididae and Tettigoniidae in Angus, Scotland." Ent. Rec. 52: 65–6.

Gives a table of comparative abundance of four species of grasshopper in waysides and fine grass, heath and coarse grass, and moor.

Thomas, I. & Jacob, F. H. (1940). "The strawberry aphis—*Pentatrichopus* (*Capitophorus*) *fragariae* Theob., with notes on *P. potentillae* Walk. and *P. tetrarhodus* Walk." Ann. Appl. Biol. 27: 234–47.

A comprehensive account of aphides found on strawberries in north Wales with special reference to the life history and populations of *P. fragariae.* A list of weeds on which this species will live is given.

Donisthorpe, H. (1940). "Strange behaviour of *Astilbus canaliculatus* F. (Col., Staphylinidae)." Ent. Mon. Mag. 76: 44.

Suggests that this beetle places dead insects in situations where they would attract ants which would be attacked and killed.

Donisthorpe, H. St J. (1940). "On the habits of *Scraptia* (Col.)." Ent. Mon. Mag. 76: 59.

This beetle breeds in wood and woody fungus and often occurs in trees infested by ants. It is found in the burrows and workings where the ants are thickest.

Hanson, H. S. (1940). "Further notes on the ecology and control of pine beetles in Great Britain." Bull. Ent. Res. 30: 483–542.

A comprehensive study which stresses the importance of studying the ecological factors associated with the host plant in addition to the factors governing the interaction of the injurious insects and their parasites and predators. Windfalls and snow-breaks provide facilities for the increase of bark-beetles. Leaving thin-barked material of small diameter lying on the ground does not cause a bark-beetle outbreak and provides for the maintenance of a permanent population of parasites and predators. The development of bark-beetle populations is discussed.

Haines, F. H. (1940). "A Tachinid (Dipt.) shelter." Ent. Mon. Mag. 76: 37.

Twelve specimens of the fly *Paraphorocera senilis* were housed between the scales of a cone of *Pinus sylvestris* in August.

Massee, A. M. (1940). "*Ceratitis capitata* Wied. (Dipt., Trypetidae) in Middlesex." Ent. Mon. Mag. 76: 112.

Two specimens of the Mediterranean fruit fly have recently been bred from home grown apples. Although frequently introduced into this country in imported fruits it has only once before (in 1869) been found breeding under natural conditions.

Niblett, M. (1940). "Gall-causing Trypetidae." Ent. Rec. 52: 13–17.

The galls of these flies are to be found in the flower heads, stems, roots and root-stocks of Composite plants. Further breeding records, ibid. 56–9.

Barnes, H. F. (1940). "The gall midges attacking the seed-heads of cocksfoot, *Dactylis glomerata*, L." Bull. Ent. Res. 31: 111–20.

An account of four species one of which is described for the first time and another which is recorded for the first time from this grass. This change of host plant in England and Ireland has not been accompanied by any change in morphological characters, whereas in New Zealand distinctive morphological characters have appeared. It is suggested that here are two steps in the evolution of a new species.

Barnes, H. F. (1939). "The chrysanthemum midge." J. R. Hort. Soc. 64: 503–6.

Life history and control methods.

Barnes, H. F. (1940). "The biology of the chrysanthemum midge in England." Ann. Appl. Biol. 27: 71–91.

A full account. A note is appended stating that this midge must now be known as *Diarthronomyia chrysanthemi* Ahlberg (1939) and the name *D. hypogaea* F.Lw. be reserved for the species found on ox-eye daisy.

Pickles, W. (1940). "The effects of ants on the acidity of soils." Ent. Mon. Mag. 76: 49–52.

Records differences in *p*H between the soils of the nests of *Lasius flavus*, *Myrmica ruginodis* and *Formica fusca* at intervals between May and October. The mounds of *L. flavus* are more alkaline than the surrounding soil and exhibit a greater difference after rain; the nests of *M. ruginodis* were also more alkaline, but those of *P. fusca* more acid.

Niblett, M. (1940). "British gall-causing Cynipidae. III." Entomologist, 73: 74–6.

An account of certain gall-causing Hymenoptera affecting plants other than oak.

Niblett, M. (1940). "Some notes on the Cynipid genus *Diplolepis*." Entomologist, 73: 145–9.

Distributional and bionomic notes on various oak gall-wasps.

Benson, R. B. (1940). "Further sawflies of the genus *Pontania* Costa (Hym., Symphyta) in Britain." Ent. Mon. Mag. 76: 88–94.

This genus now includes six leaf-edge rollers and 15 gall makers in Britain.

Benson, R. B. (1940). "On the biology of the sawfly *Xyela julii* Brébisson (Hym., Symphyta)." Ent. Mon. Mag. 76: 35–6.

A dead female was found with her ovipositor inserted into a male cone. It is suggested that the larvae feed on the staminate cones of pine, leaving them before they blossom and dropping to the ground, where they form subterranean cells.

Boycott, A. E. (1939). "Distribution and habits of *Ena montana* in England." J. Conch. 21: 153–9.

Ancient woodland on calcareous soil is the only habitat of this mollusc.

Johnson, L. R. (1940). "On the stem and bulb eelworm (*Anguillulina dipsaci* Kühn) with special reference to its occurrence on weeds of arable land." Ann. Appl. Biol. 27: 248–51.

Widespread occurrence on cleavers (*Galium aparine*) and chickweed (*Stellaria media*) in fields of eelworm-infested oats and field beans. This infestation persists in subsequent years in the fields under non-susceptible rotational crops. The weeds are capable of passing the infection to cultivated hosts and *vice versa*. The rhubarb strain of *A. dipsaci* which readily infests oats and chickweed is also capable of transference to field beans.

Scourfield, D. J. (1940). "The microscopic life of the 'leaf-carpet' of woods and forests." Essex Nat. 26: 231–46.

Coloured algae, commonly found in soils, are almost entirely absent from the permanent layer of dead leaves. The film of water between the leaves permits the existence of several microscopic aquatic organisms. Notes are given on the different groups of plants and animals found.

(*d*) Small islands

Cowin, W. S. & Williamson, K. (1940). "Manx entomological notes, 1939." Entomologist, 73: 67–8.

Records of Lepidoptera and Hymenoptera; appeals for information on insect fauna of the Island.

Harrison, J. W. Heslop (1940). "A day's collecting on the Isle of South Uist." Entomologist, 73: 1–4.

A contribution to knowledge of the insect fauna of the Outer Hebrides.

Harrison, J. W. Heslop (1940). "More Hebridean days. I: The Isle of Muldoanich and the Uidh peninsular of Vatersay." Entomologist, 73: 101–3.

Records of various insects.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Bagnall, R. S. (1940). "Notes on British Collembola." Ent. Mon. Mag. 76: 97–102.

The sixth instalment of a series of systematic papers on this obscure group of insects.

Scourfield, D. J. (1940). "Note on the difference in the coloration of the head in *Asellus aquaticus* and *A. meridianus*." Essex Nat. 26: 268–70.

The former species has two large lateral clear spaces in the posterior part of the head, *A. meridianus* has one large clear space almost across the posterior part. These constant characteristics are visible with a pocket lens: a quick substitute for high-power examination of the pleopods.

3. PARASITES

Freeman, R. B. (1940). "Siphonaptera of the Oxford district." Proc. Ashmol. Nat. Hist. Soc. 1939: 19–24.

List of species with hosts and indication of relative abundance.

Thompson, G. B. (1940). "The parasites of British birds and mammals. XXII. Additional records of *Ornithomyia* spp. from British birds, together with notes." Ent. Mon. Mag. 76: 113–16.

Records of two species of bird-flies found on 76 birds. Juvenile birds are more frequently parasitized than adults. The flies are most abundant during July and August.

Thompson, G. B. (1940). "A list of the type hosts of the Mallophaga and the lice described from them." Ann. Mag. Nat. Hist. 5: 297–308.

A useful list compiled from British Museum records.

Ritchie, J. (1940). "Sheep blowflies in Britain and their control." J. Minist. Agric. 47: 62–8.

Includes account of recent investigations and their aims, winter survivors, egg-laying and the conditions which favour it, conditions necessary for development of eggs and precautions that should be taken.

Baylis, H. A. (**1939**). "Further records of parasitic worms from British vertebrates." Ann. Mag. Nat. Hist. 4: 473–98.

An extensive list of the parasites of wild hosts, mainly birds.

Robertson, D. (**1937**). "The parasitic helminths of sheep in Scotland." Int. Congr. Zool. Lisbon, 1935, Sect. 10: 2013–44.

Questionnaires were sent out in numbers proportional to the sheep population of the counties. 54 % of the farmers suspected losses from worms; 75 % of these used anthelmintics, and with little success. A survey of 61 farms was made and worm counts are given for 33 lambs 2¾–6 months old. *Ostertagia circumcincta* was economically and pathogenically the most important species: it occurred in the fourth stomach of 32 lambs. Half of these were heavy infections, up to 17,000 worms.

Taylor, E. L. (**1939**). "Technique for the estimation of pasture infestation by Strongyloid larvae." Parasitology, 31: 473–8.

Describes method for rough estimation of number of worm larvae per pound of herbage. Samples are collected at 100 halts by two independent collectors working the pasture in a zigzag manner. Each divides his total sample into two and washes out larvae overnight. 1000 Trichostrongylid larvae are added to one part to give an estimate of percentage recovery. After filtration, larvae are recovered from sediment by a Baermann apparatus and examined microscopically. A formula is given for the estimation of the number per pound of herbage.

Evans, W. M. R. (**1940**). "Observations on the incidence of some nematode parasites of the common rabbit, *Oryctolagus cuniculus*." Parasitology, 32: 67–77.

Three species were found and their seasonal incidence is discussed with reference to its ecological implication. Using weight of rabbit as an age criterion, evidence for host and age resistance is also brought forward.

Evans, W. M. R. (**1940**). "Observations upon some common Cestode parasites of the wild rabbit, *Oryctolagus cuniculus*". Parasitology, 32: 78–90.

Six species were found. Seasonal fluctuations in their incidence are discussed, also possible span of life. In one species evidence of host and age distribution is provided. The 542 rabbits examined were obtained in a locality near Aberystwyth, north Wales.

Wells, A. Q. & Brooke, W. S. (**1940**). "The effect of vaccination of guinea-pigs with the vole acid-fast bacillus on subsequent tuberculous infection." Brit. J. Exp. Path. 21: 104–10.

Vaccination of guinea-pigs with the acid-fast bacillus of the vole (*Microtus agrestis*) prior to infection with virulent mammalian tubercle bacilli gives a degree of protection which apparently is far greater than has been recorded by other means.

Harrison, J. W. Heslop (**1940**). "A curious food-plant for *Abraxas grossulariata*." Entomologist, 73: 22.

In the Hebrides the food plant of this moth is practically always heather, although records exist for its attacking *Cotyledon umbilicus*. On Muldoanich a number of females were observed ovipositing on roseroot (*Sedum roseum*).

Donisthorpe, H. (**1940**). "*Xorides indicatorius* Latr.? parasitic on *Leiopus nebulosus* L., and a list of other species of Hymenopterous parasites of Coleoptera in Great Britain." Entomologist, 73: 14–20.

Ichneumon cocoons taken in the burrows of larvae of Longicorn beetle and a list of other Hymenopterous parasites of beetles bred, or taken with their hosts by the author in the British Isles.

Carleton, M. (1939). "The biology of *Pontania proxima* Lep., the bean gall sawfly of willows." J. Linn. Soc. (Zool.), 40: 575–624.

The life history of the sawfly is described in detail and also those of its parasites and the inquilines which inhabit the galls. Experiments on the production of artificial galls are also discussed.

Callan, E. McC. (1940). "Hymenopterous parasites of willow insects." Bull. Ent. Res. 31: 35–44.

Eight Ichneumonoidea, fourteen Chalcidoidea and six Proctotrupoidea are recorded as parasites of willow insects, the majority of the latter being found on cricket bat willow, *S. alba* var. *caerulea*.

Kerrich, G. J. (1940). "Notes on some Icheumonid and Figitid (Hym.) parasites of Neuroptera." Ent. Mon. Mag. 76: 15–17.

Parasites of the brown lace-wing *Kimminsia*.

4. FOOD AND FOOD HABITS

Baines, J. M. (1940). "Analysis of Lepidoptera eaten by bats." Entomologist, 73: 139–40.

Attacks of bats (probably common pipistrelle) on moths attracted to light in a window.

Fisher, J. (1940). "The food of wild birds." J. Soc. Pres. Fauna Emp. Part 39: 30–6.

On the basis of published estimates of the total bird population of England, Scotland and Wales and of the proportion of beneficial to harmful food habits, an attempt is made to estimate the economic status of the 29 most common land birds. The woodpigeon does most harm of all (about one-fifth of the total) and birds as a whole do about as much harm as good.

Ticehurst, C. B. (1939). "On the food and feeding habits of the long-eared owl (*Asio o. otus*)." Ibis, 3: 512–20.

An analysis of 235 whole pellets, and of fragments making an estimated total of 295 more pellets. The most noticeable result is the complete absence of shrews. Most common prey were *Microtus* (36%) and *Apodemus* (32·5%), while birds, mostly finches, composed 19·9%. These last are mostly taken in winter.

Cox, W. E. (1940). "Attacks of birds on *Pieris brassicae*." Ent. Mon. Mag. 76: 161.

On one occasion wings of at least 29 butterflies were picked up apparently dropped by house sparrows. The butterflies, their larvae and pupae had been very abundant in this locality the previous year.

Carpenter, G. D. H. (1940). "Destruction of cabbage white butterflies by birds." Nature, Lond. 145: 900–1.

As a result of the large-scale immigration into England of large cabbage white butterflies (*Pieris brassicae*) during 1939, this species was abundant during May 1940, and large numbers were destroyed by birds in both years. Counts of forewings collected during May in an Oxford churchyard established that in four days at least 54 males and 24 females were destroyed chiefly by house sparrows, but in one case by a chaffinch.

Frohawk, F. W. (1940). "Destruction of *Pieris brassicae* by birds." Entomologist, 73: 137–8.

Thirty wings found beneath a single *Buddleia*, the butterflies being caught by great-tits.

Haines, F. H. (1940). "A willow wren taking dragonflies." Ent. Mon. Mag. 76: 161.

Many teneral *Pyrrhosoma nymphula* were flying feebly by the water and being extensively attacked by a willow wren.

Rae, B. B. (1939). "Factors in the growth of lemon soles." Fisheries, Scotland, Sci. Invest., 1939, No. 3: 1–18. (Edinburgh: H.M. Stationery Office. Price 1*s*.)

The best growth zone is south of Rattray Head. Here, Polychaetes, the food-animals eaten most frequently in all zones, occupy relatively less volume in the stomach contents than in the poorer growth zones. This is because important alternative types of food are available. Further north and west these alternative foods become scarcer and the lemon sole population is higher, with the result that growth is poor.

Evans, J. D. D. (1940). "Fly life of the Usk: some speculations on its rise and fall." Salm. Trout Mag. No. 98: 36–41.

A preliminary account of the work of the Natural Fly Sub-Committee of the Usk Board of Conservators, which is investigating the food of trout and the life histories of Ephemerids of angling interest. It also contains some notes on the predatory habits of the larva of *Perla maxima* (*carlukiana*) in an aquarium.

Frost, W. E. (1939). "River Liffey survey. 2. The food consumed by the brown trout (*Salmo trutta* Linn.) in acid and alkaline waters." Proc. R. Irish Acad. 45, B: 139–206.

Brown trout from Irish waters fall roughly into two classes, small slow-growing from acid waters and large quick-growing from alkaline. The food of fish of these two groups is worked out in detail.

Pentelow, F. T. K. (1939). "The relation between growth and food consumption in the brown trout (*Salmo trutta*)." J. Exp. Biol. 16: 446–73.

A study of the growth of first and second year brown trout fed on *Gammarus pulex*. The growth in weight increases with increasing size of the fish, but there is a period of slow growth during the winter and summer. Growth is at its maximum at temperatures between 50° and 60° F. Between 40° and 50° F. the amount of growth is approximately proportional to the amount of food eaten, but above 50° F. no such simple relation exists. It is estimated that for every gram increase in weight each fish consumes between 200 and 300 *Gammarus*, whose average weight is 0·026 g.

Duddington, C. L. (1940). "Predaceous Phycomycetes from Cotswold leaf-mould." Nature, 145: 150–1.

Brief notes are given on the structure, habit and mode of reproduction of four species of Zoopagaceae (Phycomycetes) that occurred in plate-cultures inoculated with leaf-mould from Cotswold woods. The species are *Cochlonema verrucosum* and *Stylopage haploe*, parasitizing soil Amoebae; *Cochlonema dolichosporium*, parasitic on *Amoeba similis*; and *Stylopage hadra*, parasitizing Nematodes. This is believed to be the first authentic record of Zoopagaceae in England.

5. POPULATION STUDIES

Leslie, P. H. & Ranson, R. M. (1940). "The mortality, fertility, and rate of natural increase of the vole (*Microtus agrestis*) as observed in the laboratory." J. Anim. Ecol. 9: 27–52.

This paper covers part of the larger study by the Bureau of Animal Population of fluctuations in populations of voles. Out of wild stock bred in captivity 119 individuals, born at various times in the past five years, were selected at random. They include 53 males, each kept in a separate cage, 32 breeding males and 34 breeding females, the two latter groups kept paired the whole of their adult lives. The resulting life table shows an expectation of life at birth of 29·7 weeks (one lived 99 weeks). The sex ratio was approximately unity. An age-schedule of fertility gives the mean number of daughters born per 8 weeks per female. The rate of natural increase amounted to 87·7 per thousand per week which would roughly multiply the population 10 times in 6 months. The influence of an intermittent breeding season is given for lengths from 8 to 28 weeks. Environmental changes can cause violent fluctuations in numbers by comparatively small disturbances of the breeding cycle.

Hill, M. (1939). "The reproductive cycle of the male weasel." Proc. Zool. Soc. Lond. B, 109: 481–512.

The breeding season lasts from April to September. Early-born males are mature in four months, but later-born ones do not mature until the next year. Generally a weasel is mature in all respects in seven months.

Huxley, J. S. (1939). "Notes on the percentage of bridled guillemots." Brit. Birds, 33: 174–83.

Counts taken in west Scottish and Shetland colonies show that the percentage of the bridled mutant increases westwards as well as northwards. Statistical treatment of figures showing their distribution reveals varying degrees of heterogeneity. On Noss, Shetland, the distribution of the variant is very even, but on Handa, Sutherland, some sort of assortment is evident, since χ^2 has the high value of 12·727.

Hollom, P. A. D. (1940). "Report on the 1938 survey of black-headed gull colonies." Brit. Birds, 33: 202–22, 230–44.

The black-headed gull is distributed mostly in the north and west of England and Wales, the distribution of colonies showing a slight positive correlation with that of moorland. Estimated total populations are 70,000 pairs for England, and 6000 for Wales: of this Ravenglass in Cumberland contributed 50,000 pairs. Otherwise the majority of colonies fall in the 11–100 pair category. There has been a definite spread during the last 40 years, and in this time 175 places have been colonized and 70 deserted. The evidence of increase in numbers is not so clear-cut. The bulk of the paper is taken up with tabulated data for each colony.

Buxton, E. M. J. (1939). "The breeding of the oyster-catcher." Brit. Birds, 33: 184–93.

Thirty-five pairs were found breeding on Skokholm Island, Pembrokeshire (240 acres), in 1939. In 25 nests 63 eggs were laid and 88% hatched. Territory broke down, when the young began to move about, but was rigid during incubation. Birds with inland territories were thought never to visit the sea.

Alexander, W. B. (1940). "The index of heron population, 1939." Brit. Birds, 33: 304–6.

Figures over the whole of England show a slight decline in the heron population in 1939. Details show that this was most marked in southern counties and in Wales, and an actual increase is noted in the Midlands.

Colquhoun, M. K. (1940). "The density of woodland birds determined by the sample count method." J. Anim. Ecol. 9: 53–67.

The author objects to the loose use of the term census, and describes a counting method based on time as a unit, slow walking, and a random course. For an oak-ash wood on the Berkshire downs abundance of each species is tabulated per 10 hr. and compared with a complete census. A coefficient of conspicuousness is given which can be used to compute total populations from sample counts. Samples in summer should exceed 10 hr. Winter and spring counts of the 10 most abundant species in Savernake Forest are presented for fast and slow walking, the former showing 1·7 to 1 in numbers per hour. The observer's speed should be recorded.

Morley, A. (1940). "Recolonization by bird species on burnt woodland." J. Anim. Ecol. 9: 84–8.

On 200 acres of burnt forest originally containing stands of Scots pine, oak and birch, there were only two species in the first breeding season after the fire, and six species in the fourth season. On the unburnt forest 36 species were noted in 12 habitats.

Kenrick, H. (1940). "A study of blue tits by colour ringing." Brit. Birds, 33: 307–10.

Figures are given about a population of blue tits near Birmingham studied over several years. Of these three-eights were resident, one-eighth summer residents, one-quarter winter visitors and one-quarter passage migrants. Chick survival figures from nest boxes show marked variation, the average number of fledged varying from 2·4 to 4·6 in different years.

Smith, W. C. (1939). "Some notes on Irish Sea plaice." Proc. Lpool Biol. Soc. 52: 6–18.

Re-examination of data collected from 1908 to 1921 provides further knowledge of the life history.

Allen, K. R. (1940). "Studies on the biology of the early stages of the salmon (*Salmo salar*). I. Growth in the River Eden." J. Anim. Ecol. 9: 1–23.

Growth in length and weight is rapid from May to July, slows down in August in the first year and mid-July the second year, and ceases in October. Condition (weight divided by the cube of length) increases at first more rapidly than length, remains high while growth is rapid and declines when growth is slow. Activity in the spring begins at a water temperature of 7° C. Decline in growth after August is not related to food supply, as that remains constant. Most migrate in their second year, some in their first year, and the slower growing ones in their third year.

Hutton, J. A. (1940). "Wye Salmon: results of scale reading." Salm. Trout Mag. No. 98: 53–68.

Statistics of the catch, by nets and rods, of salmon in the River Wye in 1939. The total for the year was 3978 fish weighing 54,926 lb. 761 sets of scales were received for the determination of age and showed that grilse made up an unusually high proportion of the catch. The season was in general considerably better than that of 1938.

Jones, J. W. (1939). "Salmon of the Cheshire Dee, 1937 and 1938." Proc. Lpool Biol. Soc. 52: 19–80.

Data are given concerning age, weight and length, and hence condition of the fish. Comparisons are made between early and late migrants and of this population with that of other rivers.

Carpenter, J. R. (1940). "Insect outbreaks in Europe." J. Anim. Ecol. 9: 108–47.

Compilation of records of insect outbreaks for a large part of Europe, and analysis in broad regional groups based on natural vegetation, suggest that outbreaks tend to occur in the same groups of years. No regular cycles were shown. The compilations, filed elsewhere, will serve for future studies of insect populations.

Watkins, N. A. (1940). "Abundance of *Aglais urticae* last autumn, etc." Entomologist, 73: 167.

In one valley on the Wiltshire Downs this butterfly was present in hundreds for several days, but the numbers rapidly decreased.

Sandeman, R. G. (1940). "An experiment and some observations on *Vespa crabro* L. (Hymen., Vespidae)." Proc. R. Ent. Soc. Lond. A, 15: 29–32.

During the last five years the hornet has become increasingly common around Crickhowell, Breconshire. At one time it was an uncommon insect, and it was unusual to find a nest; now, however, it nests in some numbers, and seems to be increasing.

Wilson, G. Fox- (1940). "The sexual ratio of the common earwig, *Forficula auricularia* L. (Dermapt.), as observed in trap bands." Proc. R. Ent. Soc. Lond. A, 15: 17–20.

The gregarious habits of the common earwig are considered, together with the sex ratio of insects found sheltering beneath trap bands on fruit trees. The number of macrolabious forms found in the colonies is given. The limiting factor affecting the population is one of parasitism, and climatic conditions do not appear to exercise any marked influence on the number of earwigs.

Lloyd, Ll., Graham, J. F. & Reynoldson, T. B. (1940). "Materials for a study in animal competition. The fauna of the sewage bacteria beds." Ann. Appl. Biol. 27: 122–50.

Biometric observations extending over five years on the abundance of *Lumbricillus lineatus* (Enchytraeidae), *Psychoda* spp. and the chironomids *Metriocnemus* spp. and *Spaniotoma minima*.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Lloyd, L. C. (1938). "Migratory birds in Shropshire." Trans. Caradoc Fld Cl. 10: 214–36.

An abstract of 5291 observations from the club's "Record of Facts" covering the years 1892–1937. Tables show first, last and average dates on which summer and winter migrants were seen. The tendency among observers is deplored of recording unusual rather than more common events.

Southern, H. N. (1939). "The spring migration of the redstart over Europe." Brit. Birds, 33: 34–8.

The redstart spreads over Europe in 61 days (south Italy, 31 March–Inari, 15 May). Peripheral lag is noticed in the west and it is suggested that this may be due to a sparser breeding population in this part. A temperature correlation breaks down during the latter half of the spread, when the migration outstrips the spring.

Moon, H. P. (1940). "An investigation of the movements of fresh-water invertebrate faunas." J. Anim. Ecol. 9: 76–83.

In Lake Windemere and the River Avon, trays covered with substratum from which the fauna had been removed were quickly recolonized. Movement took place in winter, at water temperatures of 5 and 6° C., as well as in summer, and most of it, except for three species, occurred at night.

Edelsten, H. M. (1940). "Migration records for 1939 (*Entom.*, 72: 273)." Entomologist, 73: 21–2.

Records of butterflies and moths from the south-east coast. See also S. Swanson (1940), Entomologist, 73: 22.

Dannreuther, T. (1940). "Migration records, 1939." Entomologist, 73: 29–33.

Includes table of comparative estimates of abundance of 11 species of migrating butterflies and moths in 1939. See also supplementary list, pp. 62–3.

Dannreuther, T. (1940). "Migration records, 1940." Entomologist, 73: 110–11.

Winter records from Co. Cork, Ireland.

White, A. G. (1940). "*Vanessa cardui* hibernating in England." Entomologist, 73: 112–13.

Fourteen specimens of this butterfly were observed on 23 March which suggests that they successfully hibernated despite the severe weather.

McMillan, N. F. (1939). "Early records of *Crepidula* in English waters." Proc. Malacol. Soc. 23: 236.

Four shells from Liverpool Public Museum from Liverpool docks are dated "20/3/72"; this suggests that the species has been a member of our fauna for a longer period than has hitherto been supposed. The previous earliest record known was in 1880.

7. REPORTS OF ORGANIZATIONS

C—, H. J. (1939). "Fishery research in Scotland." Nature, Lond. 144: 487.

The Fishery Board for Scotland was started in 1882 and was the first Government department to possess a permanent scientific organization. It is now being discontinued.

Scottish Marine Biological Association (1939). Annual Report 1938–9. 47 pp.

Summaries of work in progress include the following: Studies of the relative food value of marine organisms utilized as fish food involves a knowledge of the weight, calorific value and digestibility of a wide range of species. Investigations on the life histories of six species of pelagic copepods show that the more successful and prolific broods were usually associated with the spring diatom increase; the maximum size of adults and maximum number of eggs per egg sac were found at this period of plentiful diatom food. The macrofauna in a variety of intertidal and sublittoral deposits is being quantitatively investigated.

Freshwater Biological Association of the British Empire (1940). Eighth Annual Report for the year ending 31 March 1940. 81 pp. Price to non-members 1*s.* 6*d.* (Address: Wray Castle, Ambleside, Westmorland.)

This report differs from last year's in containing no semi-popular accounts of the work in progress by members of the staff. The Director's report, however, gives a good account of the work done during the year. With the outbreak of war the economic aspects of fresh-water biology, particularly fisheries and water supply, came into greater prominence. Work was carried out on salmon, brown trout, rainbow trout, eels, perch, minnows and other coarse fish, on the use of fertilizers to improve fisheries, on invertebrate animals, algae, bacteriology and on hydrography, chemistry and lake deposits. The Association has taken over the work formerly carried out by the Avon Biological Survey at Southampton.

Wye Board Conservators (1940). Annual Report Season 1939. 16 pp.

An account of the salmon fishery in the Wye during 1939, with statistics of the catch of various size classes of fish for this and previous years. Includes also information on spawning of salmon, on trout fishing, on pollution and on administrative matters connected with the fishery.

Yorkshire Fishery District, Board of Conservators (1940). Seventy-third Annual Report on the Salmon, Trout and Freshwater Fisheries in Yorkshire (by R. W. Ward). 36 pp.

Gives figures for the catch in 1939, by nets and rods, in sea, estuary and river, of salmon (1096 fish weighing 16,109 lb.) and migratory trout (1367 fish weighing 5519½ lb.). Notes are included on brown trout and other fresh-water fish, fish passes, restocking, the Keld Head hatchery and pollution.

Skokholm Bird Observatory (1940). Report for 1939. 12 pp. (Address: Skokholm Bird Observatory, Dale, Haverfordwest, Pembrokeshire, Wales.)

The great reduction in rabbit numbers by cyanide gassing is reported to have had far-reaching effects on the vegetation. Hay was cut for the first time in 12 years, and sheep were introduced. House mice were abundant, and short-eared owls appeared. The rabbit-breeding season is also said to have been extended. Turned down canaries were mostly killed by sparrowhawks. 5489 shearwaters were ringed, and further birds have homed from Stratford-on-Avon, Lugano and Berne.

Bulletin of the British Ornithologists' Club. No. 427 (1940). 60: 27–43.

Mentions recent activities of British and American ornithologists. A. Landsborough Thomson reviews some of the work on periodicity in birds. A summary of the world gannet population counts is given.

Natural history notes for the district with the Proceedings of the Liverpool Naturalists' Field Club (1940). 28 pp. Price (to non-members), 1*s.* (Address: 5 Parkfield Drive, Wallasey.)

Notes on the fauna, particularly shearwaters, of Bardsey Isle. Among winter migrants to Hilbre Island and the Dee estuary are many birds that come south-west from the Arctic: 300 scaup were to be seen from Christmas to March 1939. Observations on 77 species of birds are listed.